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Population structure of the corals *Orbicella faveolata* and *Acropora palmata* in the Mesoamerican Barrier Reef System with comparisons over Caribbean basin-wide spatial scale

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Abstract Studies of genetic diversity and population genetic structure in marine organisms are relevant to understanding populations' variability, and therefore their ability to withstand environmental perturbations, their potential for resistance to local extinction and their natural rate of recovery. Population structure and genetic diversity were assessed at a regional spatial scale (i.e., Mesoamerican Barrier Reef System, MBRS) in two major reef building coral species *Orbicella* (formerly *Montastraea*) *faveolata* and *Acropora palmata*, and at a larger spatial scale (i.e., Caribbean-wide; MBRS, Panama, Venezuela and Puerto Rico) for *A. palmata* only. The most significant findings were as follows: (1) high genetic diversity and low clonality were found for both species, which is expected for *O. faveolata* but not for *A. palmata*, (2) both species showed low-to-moderate, yet significant population structure among populations along the MBRS; in particular, *O. faveolata* and *A. palmata* from Ambergris (Belize) and *O. faveolata* from Calabash (Belize) and *A. palmata* from Puerto Morelos (Mexico) showed some genetic differentiation from the rest of the MBRS populations, and (3) *A. palmata* from MBRS, Panama, Puerto Rico and Venezuela were grouped into four subregions that could be considered as management units. A more spatially detailed sampling program and the inclusion of recruits will be necessary to get a comprehensive understanding of coral population structure and current gene flow patterns in these two species.

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Introduction

Coral reefs have been declining dramatically world-wide due to multiple stressors including habitat loss, overfishing, pollution, tourism (Jackson et al. 2001; Kramer and Kramer 2002), the increasing prevalence of diseases (Harvell et al. 1999; Garzón-Ferreira et al. 2001; Cróquer and Weil 2009) and bleaching (Hoegh-Guldberg et al. 2007; Carilli et al. 2009). The combination of the devastating effects of these factors has challenged coral reef resilience, particularly in the Caribbean, where extensive degradation of reef habitats has been reported (Hughes 1994; Hughes and Tanner

2000; Gardner et al. 2003; Bellwood et al. 2004; Bak et al. 2005; Edmunds and Elahi 2007; Carilli et al. 2009). The Mesoamerican Barrier Reef System (MBRS) is the largest barrier reef in the Caribbean, extending over 1,000 km, and includes reefs of Mexico (Yucatán Peninsula), Belize, Guatemala and Honduras. Although it is recognized as a major biodiversity region (Kramer and Kramer 2002; McField et al. 2008), recent rapid declines with little recovery in coral populations have been documented (Aronson et al. 2000; McField et al. 2008; Rodríguez-Martínez et al. 2014).

Determining genetic diversity and population structure is important for management and conservation of coral reef systems. These data can provide an understanding of the natural populations' genetic variability and therefore, their ability to withstand environmental perturbations, their potential for resistance to local extinction and their natural rate of recovery (reviewed in van Oppen and Gates 2006). Furthermore, genetic diversity and population structure are key elements in evaluating and predicting the impacts of population declines (Haig 1998; Petit et al. 1998; Reed and Frankham 2003; Pérez-Ruzafa et al. 2006; Baums 2008; DiBattista 2008).

Many marine organisms have pelagic larvae that travel for long distances with oceanic currents promoting the exchange of new recruits (Roberts 1997). Significant and positive correlations between the duration of planktonic phases and the dispersal distance for 32 marine taxa have been found (Shanks et al. 2003; Shanks 2009). However, genetic studies indicate that the actual dispersal of some species can be more complex depending on factors other than duration in the plankton, and possibly operating at different temporal and spatial scales (e.g., Cowen et al. 2006; Levin 2006). For example, whole or partial colony mortality, as well as fragmentation and fission, can reduce the overall reproductive output of coral populations leading to a decreased larval supply. Additionally, systematic or chronic mortality may increase distance between colonies, reducing fertilization success and larval production in some species (e.g., Allee effect; Courchamp et al. 1999). With a decreased larval supply, local recruitment and dispersal to non-local populations may be reduced, with a concomitant decrease in biological connectivity and gene flow among and between once-connected populations (Hughes and Tanner 2000; Zakai et al. 2000; Okubo et al. 2007). Successful recruitment of distantly dispersed larvae is likely to be a rare event, and rarer today with the probability of a reduced larvae supply. Lastly, population genetic structure can change with scale because the landscape can introduce physical barriers that can affect gene flow (Anderson et al. 2010).

Different levels of population structure and gene flow among Caribbean fish, soft corals, sponges and other invertebrate taxa have been reported (e.g., Mitton et al. 1989; Duffy 1993; Shulman and Bermingham 1995; Lessios et al. 1999, 2001, 2003; Rocha et al. 2002; Taylor and Hellberg 2003; Gutiérrez-Rodríguez and Lasker 2004; Bowen et al. 2006; Ospina-Guerrero et al. 2008; Hepburn et al. 2009; Sala et al. 2010; Andras et al. 2013; Prada and Hellberg 2013). Studies of genetic diversity and population structure are especially relevant for keystone and structural coral species as they contribute the majority of the reef framework, providing shelter and habitat complexity for many other reef species.

In the Caribbean, two coral species, the elkhorn coral *A. palmata* and the boulder star coral *Orbicella faveolata* (previously classified as *Montastraea*; Budd et al. 2012), are particularly important in creating reef structure; however, they have suffered dramatic population reduction during the last decades. Currently *A. palmata* is listed as critically endangered and *O. faveolata* as endangered under the International Union for the Conservation of Nature Red List criteria (Aronson et al. 2008). *A. palmata* was the major Caribbean reef builder in high-energy environments before a wide-spread epizootic event severely reduced their populations across the region (Gladfelter 1982; Bythell and Sheppard 1993; Aronson and Precht 2001). A recent study evaluating the recovery of *A. palmata* along the MBRS concluded that this species has failed to recover to pre-1980s population size and geographic distribution (Rodríguez-Martínez et al. 2014). *O. faveolata* is distributed across the Caribbean region over a range of depths and accounted for over 50 % of the live coral cover in many locations (Cortés 2003). However, recent epizootics of wide-spread coral diseases (e.g., white plague and yellow band) and bleaching events have decreased their population numbers dramatically and compromised their reproductive output (Knowlton et al. 1992; Bruckner and Bruckner 2006; Miller et al. 2006; Bruckner and Hill 2009; Weil et al. 2009). *O. faveolata* has also suffered significant population reductions along the MBRS (Mcfield et al. 2008).

Despite the importance of these coral species, only a few studies have evaluated their patterns of genetic structure in the greater Caribbean Region. Baums et al. (2005a) found that *A. palmata* has experienced little or no recent gene flow between eastern (US Virgin Islands, St. Vincent and the Grenadines, Bonaire and Curacao) and western (Panama, Mexico, Florida, the Bahamas and Navassa) Caribbean populations. Later, at smaller spatial scales, Zubillaga et al. (2008) found low-to-moderate population structure among populations of Los Roques (Venezuela). Population genetic studies of *Acropora cervicornis*, sister taxa of *A. palmata*, found significant population genetic structure across the greater Caribbean Region (Vollmer and Palumbi 2007; Baums et al. 2010) and no evidence for population genetic structure along the Florida reef track (Baums et al. 2010).

Only two studies have evaluated patterns of population structure for *O. faveolata,* and both found no evidence of population differentiation among Puerto Rico, lower Florida Keys and the Yucatan Peninsula populations (Severance and Karl 2006) nor within the Florida reef track and between Florida and Mexico populations (Baums et al. 2010). On the other hand, *O. faveolata*'s sister taxa *O. annularis*, also a broadcast spawner, showed strong population differentiation among Puerto Rico, lower Florida Keys and the Yucatan Peninsula populations (Severance and Karl 2006). Furthermore, populations of *O. annularis* are genetically differentiated into three regions in the greater Caribbean: eastern (Lesser Antilles, Venezuela and Curacao), western (the Bahamas, Cuba, Belize and Cayman Islands) and central (Jamaica, Honduras, Nicaragua, Colombia, Puerto Rico, British Virgin Islands and Dominican Republic) (Foster et al. 2012). None of the previous studies on genetic population structure for *A. palmata* and *O. faveolata* have extensively sampled along the MBRS. Genetic connectivity within the MBRS has only been evaluated for coral reef fish (Hepburn et al. 2009; Puebla et al. 2012) and *O. annularis* (Foster et al. 2012).

The primary goals of this study were to determine and contrast *O. faveolata* and *A. palmata* patterns of population genetic structure and genetic diversity at regional scale (i.e., MBRS) and to determine population structure at large scales (i.e., Caribbean-wide) for *A. palmata*. Population genetic structure of *O. faveolata* and *A. palmata* were determined using four species-specific microsatellite loci for *A. palmata* (Baums et al. 2005b) and six microsatellite loci for *O. faveolata* which were previously developed for the sibling species *O. annularis* (Severance et al. 2004). Six sites for both species were sampled along the MBRS (Mexico and Belize). Furthermore, for *A. palmata,* another six sites across the Caribbean were also sampled (two sites within each country: Venezuela, Puerto Rico and Panama). Given previous studies on population genetics of both species and reproductive characteristics (e.g., broadcast spawners and long competency period), low-to-no population structure was expected among *O. faveolata* and *A. palmata* populations along the MBRS. Furthermore, *A. palmata* populations were expected to be divided into west and east Caribbean subregions. Following a spatial hierarchical approach and including several locations along the MBRS provided a more informative database for regional planning and local conservation of these structural coral reef species.

Methods

Sample collection

In order to assess the genetic diversity and population structure of *O. faveolata* and *A. palmata*, a total of 473 *O. faveolata* and 551 *A. palmata* mid-size adult (non-remnant 20–100 cm maximum diameter) and adult (>100 cm maximum diameter) colonies were collected from various sites along the MBRS (Mexico and Belize). In addition, 481 *A. palmata* colonies were sampled at two sites each in Panama, Venezuela and Puerto Rico, allowing for comparisons at Caribbean basin-wide metapopulation scale (>1,000 km) (Fig. 1; Table 1; Online Resource 1). At each site, colonies at least 5 m apart were sampled to minimize the collection of clones or fragments of the same colony.

Each site was sampled over an area of 1 km^2 and at depths ranging from 1 to 15 m. To prevent sampling possible hybrids within the *O. annularis* sibling species complex (Knowlton et al. 1992; Weil and Knowlton 1994; Szmant et al. 1997), colonies with intermediate phenotypes were avoided. From each colony, ca. 1 cm^2 of live tissue was removed and preserved in 95 % ethanol for *A. palmata* and in high salt solution (20 % DMSO, 250 mM EDTA, NaCl-saturated) for *O. faveolata*.

Laboratory analysis

Genomic DNA was extracted from coral tissue samples using a DNeasy Tissue Extraction kit (Qiagen) and, in the case of *O. faveolata*, purified following a polyethylene glycol protocol. Genetic characterization of the populations from both species was determined using species-specific microsatellite loci for *A. palmata* (Baums et al. 2005b) and microsatellite loci previously developed for the sibling species *O. annularis*, for *O. faveolata* (Severance et al. 2004). After screening all loci in Baums et al. (2005b) and six out of seven (see below) from Severance and Karl (2006), four loci and five loci were deemed usable for *A. palmata* and *O. faveolata,* respectively. The microsatellite locus MS2-17, previously designed by Severance et al. (2004), was not included since the authors showed that it amplified some *O. faveolata* individuals less efficiently (Severance and Karl 2006). Furthermore, locus MaMS12 demonstrated a high frequency of null alleles and consistent heterozygote deficit across all populations (data not shown) and was also excluded. Genotypic data from 5 microsatellite loci for *O. faveolata* and four loci for *A. palmata* are available as Online Resource 2 and 3, respectively.

Each microsatellite locus was amplified via a polymerase chain reaction (PCR) in a 10-µl reaction containing the following final concentrations: 0.2 mM dNTPs, 10 mM Tris–HCl buffer (pH 8.3), 50 mM KCl, 2.5–3 mM $MgCl_2$, 0.2 µM each fluorescently labeled primer, 1 U Taq polymerase and 10–20 ng DNA template. Thermal cycling conditions for *A. palmata* loci consisted of an initial denaturation step for 5 min at 95 °C, followed by 35 cycles at 95 °C for 20 s, 47–53.1 °C for 20 s and 72 °C for 30 s with a 30-min final extension at 72 °C (Baums et al. 2005b).

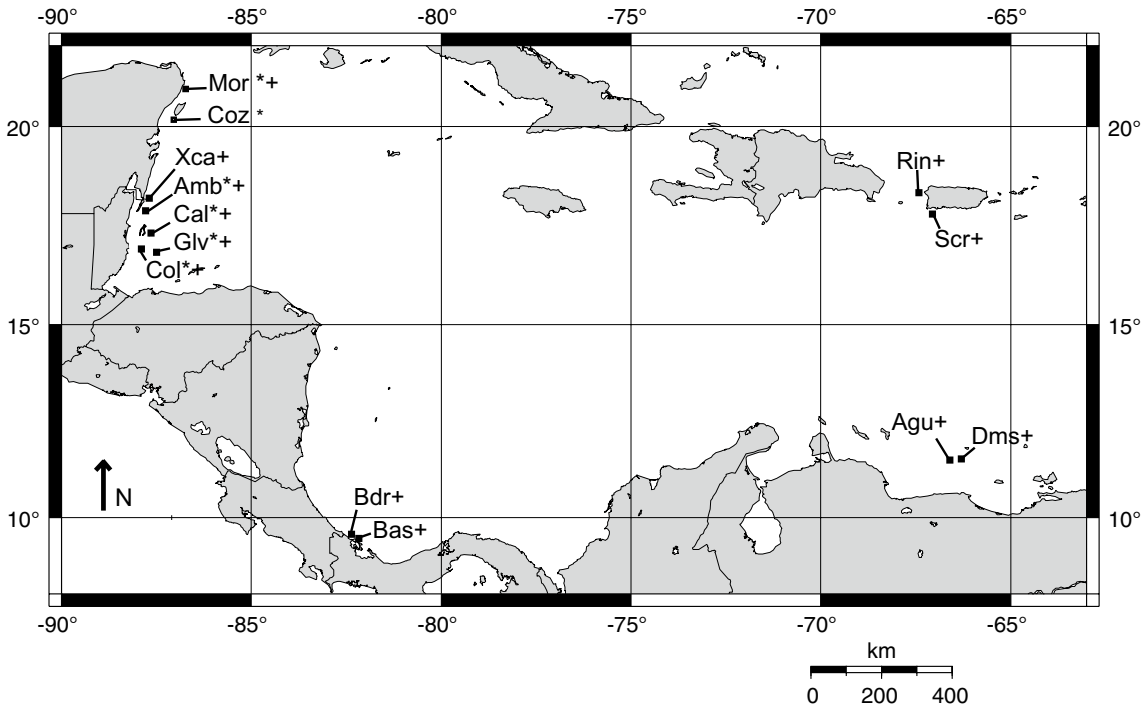

Fig. 1 Sampling locations of *Orbicella faveolata* (*) and *Acropora palmata* (+). Mexico populations include Puerto Morelos (Mor), Cozumel (Coz), and Xcalak (Xca); Belize population include Ambergris (Amb), Calabash Cay (Cal), Columbus Reef (Col) and Glovers Reef (Glv); Panama populations include Bocas del Drago (Bdr) and Bastimento (Bas); Venezuela population include Cayo de Agua (Agu) and Dos Mosquises (Dms); Puerto Rico include Rincón (Rin) and San Cristobal (Scr). Map was created at http://www.aquarius.geomar.de/omc/

Table 1 *Orbicella faveolata* and *A. palmata* sampling locations, sample sizes (no. of colonies), number of genets and proportion of unique genotypes

Country	Site	*O. faveolata*			*A. palmata*		
		No. of colonies (N)	No. of genets (N_g)	N_g/N	No. of colonies (N)	No. of genets (N_g)	N_g/N
Mexico	Puerto Morelos (Mor)	42	42	1	105	92	0.88
	Cozumel (Coz)	32	32	1	N/A	N/A	N/A
	Xcalak (Xca)	N/A	N/A	N/A	49	48	0.98
Belize	Ambergris (Amb)	99	95	0.97	99	94	0.95
	Turneffe (Cal)	101	97	0.96	79	68	0.86
	Glovers (Glv)	103	103	1	104	102	0.98
	Columbus (Col)	96	96	1	115	111	0.97
Panama	Bocas del Drago (Bdr)	N/A	N/A	N/A	80	60	0.75
	Bastimento (Bas)	N/A	N/A	N/A	80	58	0.73
Venezuela	Dos Mosquises (Dms)	N/A	N/A	N/A	113	106	0.94
	Cayo de Agua (Agu)	N/A	N/A	N/A	100	86	0.86
Puerto Rico	San Cristóbal (Scr)	N/A	N/A	N/A	39	26	0.67
	Rincón (Rin)	N/A	N/A	N/A	69	45	0.65
Total		473	465		1,032	896	

MBRS, Mesoamerican Barrier Reef System; Genotypic richness, N_g/N = number of genets/number of sampled colonies (ramets) abbreviations for sites are in parentheses; N/A = site not sampled

Thermal cycling conditions for *O. faveolata* consisted of an initial denaturing period of 2 min at 95 °C, followed by 40 cycles at 95 °C for 1 min, 50–55 °C for 40 s and 72 °C for 1 min and a final extension period of 30 min at 72 °C. All PCR amplifications for both species were carried out in an Eppendorf Mastercycler Gradient thermal cycler in Dr.

T.W. Snell laboratory at Georgia Institute of Technology (Atlanta, GA).

For both species, fluorescently labeled products were analyzed on an ABI 3730xl automated sequencer (Nevada Genomics Center, University of Nevada, Reno) and allele sizes were determined relative to an internal size standard (Gene Scan 500-Liz; Applied Biosystems) from resulting electropherograms using PeakScanner version 1.0 (Applied Biosystems).

Population genetics and statistical analyses

Allelic richness and heterozygosity values are reported in this study, but allelic richness was preferred as a measure of genetic diversity because it may reflect more effectively a population's long-term evolutionary potential than would heterozygosity (e.g., Allendorf 1986; Petit et al. 1998). To avoid biased comparisons of allelic richness among populations due to unequal sample sizes (Petit et al. 1998; Leberg 2002), a rarefaction procedure was conducted for each population using FSTAT version 2.9.3.2 (Goudet 1995, 2002), based on minimum sample sizes of 15 (*O. faveolata*) and 39 (*A. palmata*) diploid individuals. However, the total number of alleles per locus/population and private alleles per population were also calculated.

Because identical multilocus genotypes were found in both species, the probability of identity (P_{ID}), the average probability that two unrelated individuals drawn from the same randomly mating population will have the same genotype by chance, was calculated in GenAlEx version 6.5 (Peakall and Smouse 2006, 2012). Furthermore, assignment of individuals to clonal lineages was performed in GenoDive version 2.0b23 (Meirmans and Van Tienderen 2004). Assignment of clones was carried out by calculating a distance matrix, which is the maximum distance between two individuals that are considered to belong to the same lineage. The pairwise distance between colonies was calculated assuming an infinite allele model of evolution. The optimum threshold (e.g., maximum pairwise distance between two colonies so these will be considered clonemates) could be determined based on a frequency distribution of pairwise distance (Rogstad et al. 2002). Often, the pairwise distance histogram is multinomial and should show a gap between clones and full siblings; however, due to the low number of clones and possibly due to a low number of loci, this gap was not evident for either species (Online Resource 4). Threshold (pairwise distance) = 0, corresponds to identical genotypes. For a sexual species that can reproduce asexually like *A. palmata*, threshold = 1 may represent distances between different ramets from the same individual (genet), that differ due to scoring errors or, less likely, somatic mutations (Meirmans and Van Tienderen 2004). *O. faveolata* colonies that had missing data were not included in this analysis but were included in further analysis. Using threshold = 1 for *A. palmata* and threshold = 0 for *O. faveolata*, a total of 136 for *A. palmata* and 8 *O. faveolata* individuals that had identical or nearly identical multilocus genotypes were eliminated from subsequent analysis (Table 1). For *A. palmata,* a threshold = 0 was initially selected; however, after eliminating all the clonemates with only identical multilocus genotypes, significant linkage disequilibrium (LD) was observed in 25 % of pair comparisons between loci.

Allele frequencies, LD between all pairs of loci per population, observed and expected heterozygosity and deviations from Hardy–Weinberg equilibrium (F_{IS} fixation index; Wright 1965) for each population and at each locus were calculated using FSTAT version 2.9.3.2 (Goudet 1995, 2002). The proportion of randomization that gave a larger F_{IS}-value than the observed was used to test for significant deviations from Hardy–Weinberg equilibrium.

The presence of null alleles within the populations of both species and F_{ST} analysis with and without null allele correction was evaluated with FreeNA (Chapuis and Estoup 2007). For the remaining five *O. faveolata* loci, the corrected F_{ST} value in the presence of null alleles did not differ (difference in F_{ST} = 0.0001–0.0077; Online Resource 5) from the non-corrected F_{ST} value, suggesting that null alleles do not have a large impact in the calculation of F_{ST}, therefore the original data set was used in further analysis.

To assess genetic differentiation among populations of the two species, estimators of F_{ST} were calculated in FSTAT version 2.9.3.2 (Goudet 1995, 2002) following Weir and Cockerham (1984). R_{ST} estimators were also calculated in RstCalc (Goodman 1997), but values did not differ from those obtained by F_{ST} (data not shown).

Genetic variance among populations was visualized in GenAlEx version 6.5 (Peakall and Smouse 2006, 2012) through Principal Coordinates Analysis (PCoA) of pairwise genetic distances. PCoA is a multivariate technique that allows visualization of major patterns within a multivariate data set. The analysis was run using the F_{ST} values calculated in FSTAT version 2.9.3.2 (Goudet 1995, 2002) and selecting 'Distance-Not Standardized' option.

To evaluate whether genetic distance is correlated with geographic distance, $F_{ST}/(1 - F_{ST})$ and log of geographic distance were plotted and a Mantel test was performed using GenAlEx version 6.5 (Peakall and Smouse 2006, 2012). In the case of *A. palmata,* this test was performed not only at regional scale (i.e., MBRS) but also at a larger spatial scale (i.e., Caribbean-wide).

We estimated admixture among *A. palmata* and *O. faveolata* populations by applying a Bayesian model-based clustering algorithm implemented in the program STRUCTURE version 2.3.3 (Pritchard et al. 2000; Falush et al. 2003, 2007). The admixture model was chosen with

correlated allele frequencies between populations. The analysis was performed using LOCPRIOR model and the standard method (not using population location as a priori). LOCPRIOR uses the sampling locations to assist the clustering process (Hubisz et al. 2009). The number of ancestral clusters, K, was determined by comparing the likelihood values between 10 independent replicate runs of K from 1 to 12 for *A. palmata* and 1 to 6 for *O. faveolata*. The length of the burn-in was 100,000, and the number of MCMC replications after the burn-in was 500,000. The number of K's used corresponded to the total number of populations that were sampled, where $K = 1$ implies no population structure and $K =$ maximum number of populations implies that each population is differentiated. The best estimate of K was calculated using Structure Harvester (Earl and von Holdt 2012) following the ad hoc statistic ΔK (Evanno et al. 2005) and by plotting the maximal value of the probability of the data, Ln $Pr(X|K)$, against a range of K. The best estimate of K is that where Ln $Pr(X|K)$ is the maximum or the one after the trend plateaus (Pritchard et al. 2000, 2010).

Hierarchical partitioning of genetic variation was determined via analysis of molecular variance (AMOVA) in Arlequin version 2.0 (Schneider et al. 2000). Total genetic variation was partitioned into three levels: among regions (guided by the final number of ancestral clusters, K, see above), among populations within regions and within populations.

Table 2 Summary statistics per population for (a) five microsatellite loci for six populations of *O. faveolata*, (b) four microsatellite loci for 12 populations of *A. palmata*

Population	H_o	H_e	F_{IS}	P_{ID}
(a) *Orbicella faveolata*				
Mor	0.602 (0.120)	0.657 (0.105)	0.097	1.7E−05
Coz	0.568 (0.138)	0.632 (0.107)	0.123	4.8E−05
Amb	0.590 (0.099)	0.739 (0.070)	0.208*	2.0E−06
Cal	0.600 (0.111)	0.752 (0.073)	0.202*	1.1E−06
Glv	0.616 (0.101)	0.647 (0.098)	0.053	2.7E−05
Col	0.590 (0.107)	0.671 (0.095)	0.127*	1.7E−05
(b) *Acropora palmata*				
Mor	0.967 (0.000)	0.900 (0.013)	−0.069	9.9E−08
Xca	0.922 (0.032)	0.892 (0.016)	−0.023	1.3E−07
Amb	0.949 (0.018)	0.889 (0.010)	−0.063	1.9E−07
Cal	0.868 (0.044)	0.885 (0.029)	0.028	1.6E−07
Glv	0.904 (0.021)	0.890 (0.017)	−0.012	1.5E−07
Col	0.890 (0.012)	0.887 (0.019)	0.002	1.8E−07
Bdr	0.946 (0.013)	0.880 (0.010)	−0.066	5.2E−07
Bas	0.957 (0.023)	0.898 (0.006)	−0.057	2.1E−07
Dms	0.788 (0.064)	0.799 (0.063)	0.019	4.7E−06
Agu	0.761 (0.085)	0.797 (0.064)	0.050	7.1E−06
Scr	0.885 (0.027)	0.849 (0.032)	−0.022	1.6E−06
Rin	0.906 (0.059)	0.859 (0.05)	−0.043	6.0E−07

H_e = expected heterozygosity, H_o = observed heterozygosity, F_{IS} = inbreeding coefficient, P_{ID} = probability of identity for each locus and population

* Statistically significant F_{IS} values after corrections for multiple comparisons by Bonferroni. Significant P values obtained after 600 for *O. faveolata* and 960 permutations for *A. palmata*, indicative adjusted nominal level (5 %) for multiple comparisons is: 0.00167 for *O. faveolata* and 0.00104 for *A. palmata*

Results

Allelic diversity

Measures of average allelic richness for *O. faveolata* showed that the number of alleles per locus within each population ranged from 3.0 to 12.9 (calculated for 15 sampled individuals, rarefaction correction for unequal sampling size, see methods; Online Resources 6). The most common allele for each locus also differed among populations (Online Resource 6). For *O. faveolata*, departure from Hardy–Weinberg equilibrium was found in three Belize populations: Ambergris, Calabash Cay and Columbus (Table 2a). The presence of null alleles could not be discounted as an explanation for this significant deficiency; these three populations had the highest incidence of putative null alleles (Online Resource 5), which may contribute to their positive inbreeding coefficients (F_{IS}). Evidence of null alleles was also found in six population/locus combinations that did not demonstrate significant heterozygote deficits. Significant LD was detected in 5 % (3 of 60) of pair comparisons between loci after sequential Bonferroni correction (Online Resource 7), but these LDs were inconsistent across populations, thus physical linkage could be discounted and these loci were considered to be independent.

For *A. palmata*, measures of average allelic richness showed that the number of alleles per locus within each population ranged from 8.654 to 18.193 (calculated for 39 sampled individuals, rarefaction correction for unequal sampling size, see methods; Online Resource 6) and the most common allele for each locus differed among populations (Online Resource 6). Populations were in Hardy–Weinberg equilibrium (Table 2b). Significant LD was detected in 5.5 % (4 of 72) of pair comparisons between loci after sequential Bonferroni correction (Online Resource 7). The frequency of null alleles was low (0.00001–0.07) at all four loci across the 12 populations.

Both *O. faveolata* and *A. palmata* populations were characterized by a high proportion of unique genotypes or genets (0.96–1.00 and 0.65–1.0, respectively; Table 1); however, higher clonality (i.e., lower genotypic richness, N_g/N)

was observed in Puerto Rico (Scr = 0.67, Rin = 0.65, Table 1) and in Panama (Bdr = 0.75, Bas = 0.73; Table 1). The probability of identity (P_{ID}) for both species (Table 2, Online Resource 6) was very low.

Orbicella faveolata and *Acropora palmata* population genetic structure along the Mesoamerican Barrier Reef System

Orbicella faveolata and *A. palmata* global F_{ST} values were low but significant (F_{ST} = 0.0189 and 0.0037, $P < 0.001$, respectively), rejecting the null hypothesis of complete panmixia among the populations along the Mesoamerican Barrier Reef System (MBRS). Furthermore, the genetic structure observed for *O. faveolata* and *A. palmata* in the MBRS was not explained by the isolation-by-distance model (Mantel test, *O. faveolata*, $r = 0.094$, $P = 0.380$ and *A. palmata*, $r = 0.328$, $P = 0.300$; Fig. 2a). Although population pairwise F_{ST} comparisons were very low for *A. palmata* ($F_{ST} < 0.009$, Table 3a), several values were significant, suggesting minimal levels of gene flow restriction.

In general, *O. faveolata* and *A. palmata* PCoA (Fig. 3a, b) showed similar patterns of relative genetic similarity among populations within the MBRS. For both species, Amb (Belize) is clearly differentiated from the rest of the populations. However, the *O. faveolata* Cal (Belize) population was not genetically differentiated from Amb (Belize), while these two populations were separated from other populations sampled in Belize and Mexico (Fig. 3a). Also, *A. palmata* from Mor (Mexico) was different from the rest of the populations (three genetic clusters were observed for this species; Fig. 3b), in agreement with the pattern of low but significant F_{ST}.

The number of ancestral clusters calculated in STRUCTURE version 2.3.3 for *O. faveolata* was $K = 2$ based on the ΔK method and Ln $Pr(X|K)$ (Fig. 4a; Online Resource 8), whereas for *A. palmata,* the most likely number of clusters was $K = 1$ based on Ln $Pr(X|K)$. Although suggested by the ΔK method, $K = 2$ (noLOCPRIOR) and $K = 5$ (LOCPRIOR) were not supported by the group membership coefficients (Online Resource 8). Furthermore, ΔK method (Evanno et al. 2005) often fails to find $K = 1$ when population structure is absent.

The analysis for *A. palmata* is, nonetheless, affected by the a priori assignment of the samples based on the collection sites' information. Bayesian cluster analysis ($K = 5$, LOCPRIOR) recovered genetic clusters that perfect match localities with a significant F_{ST} between them (with the exception of Xca and Cal that formed a unique cluster). However, when locality information was removed, only one panmictic population without isolation by distance was obtained (Figs. 2b, 5a).

AMOVA of *F*-statistics for *O. faveolata* and *A. palmata* partitioned the majority of the genetic variance (96.55 and 99.62 %, respectively; Table 4) to variation within populations being significant at this scale (F_{ST} = 0.034 and F_{ST} = 0.0038 $P < 0.0001$; Table 4), and not between regions or populations (Table 4).

Genetic population structure of *Acropora palmata* at regional and Caribbean-wide spatial scale

Global F_{ST} was low but significant (F_{ST} = 0.0232, $P < 0.001$), and the overall observed genetic structure of *A. palmata* at large scales could be explained by the isolation-by-distance model (Wright 1943), as a significant correlation was found between genetic distance and geographic distance (Mantel test, $r = 0.549$, $P = 0.001$; Fig. 2b). Less population differentiation was found between geographically close populations, such as those within the MBRS (see above) and Puerto Rico (Table 3b) with increasing differentiation between more distant populations, such as between Mor (Mexico) and Agu (Venezuela) (~2,350 km; Fig. 2b). However, small but significant pairwise F_{ST} values were found between population Agu and Dms (Venezuela), which are 5 km apart, and between Bas and Bdr (Panama), which are 16 km apart (Table 3a; Fig. 2b).

PCoA based on F_{ST} measures (Fig. 3c) and Bayesian cluster analysis with and without a priori location information (Fig. 5a, b; Online Resource 9) recovered two major groups: The first grouped all the populations from Venezuela (Dms and Agu) and the second was formed by the remaining populations (MBRS, Panama and Puerto Rico). However, the plot of Ln $Pr(X|K)$ and the ΔK using LOCPRIOR (Online Resource 9) were multimodal, which suggests multiple solutions (Pritchard et al. 2010). The Ln $Pr(X|K)$ plot started low at $K = 1$, then rose sharply to $K = 2$ and then to $K = 4$ before descending and then rising again at $K = 8$, and $K = 10$. Evanno et al. (2005) found that once the true value of K is reached, Ln $Pr(X|K)$ plateaus or continues slightly increasing at larger values of K, which is the pattern observed here suggesting that $K = 8$ and 10 may not be real solutions of K. Based on group membership coefficients, $K = 2$ (Fig. 5a, b) and $K = 4$ (Fig. 5c) are the most likely number of clusters. To further investigate $K = 4$, 8 or 10, a cluster analysis (without Venezuela) was conducted using STRUCTURE version 2.3.3 (Pritchard et al. 2000; Falush et al. 2003, 2007). The cluster formed by MBRS, Panama and Puerto Rico was analyzed following the same parameters used for the initial Bayesian cluster analysis. Based on ΔK and the plot of Ln $Pr(X|K)$, $K = 3$ was the most likely number of clusters (Online Resource 9). One cluster grouped all the populations from the MBRS, and the second included populations from Panama and the populations from Puerto Rico formed the third cluster (Fig. 5d; Online Resource 9). Furthermore, a PCoA excluding

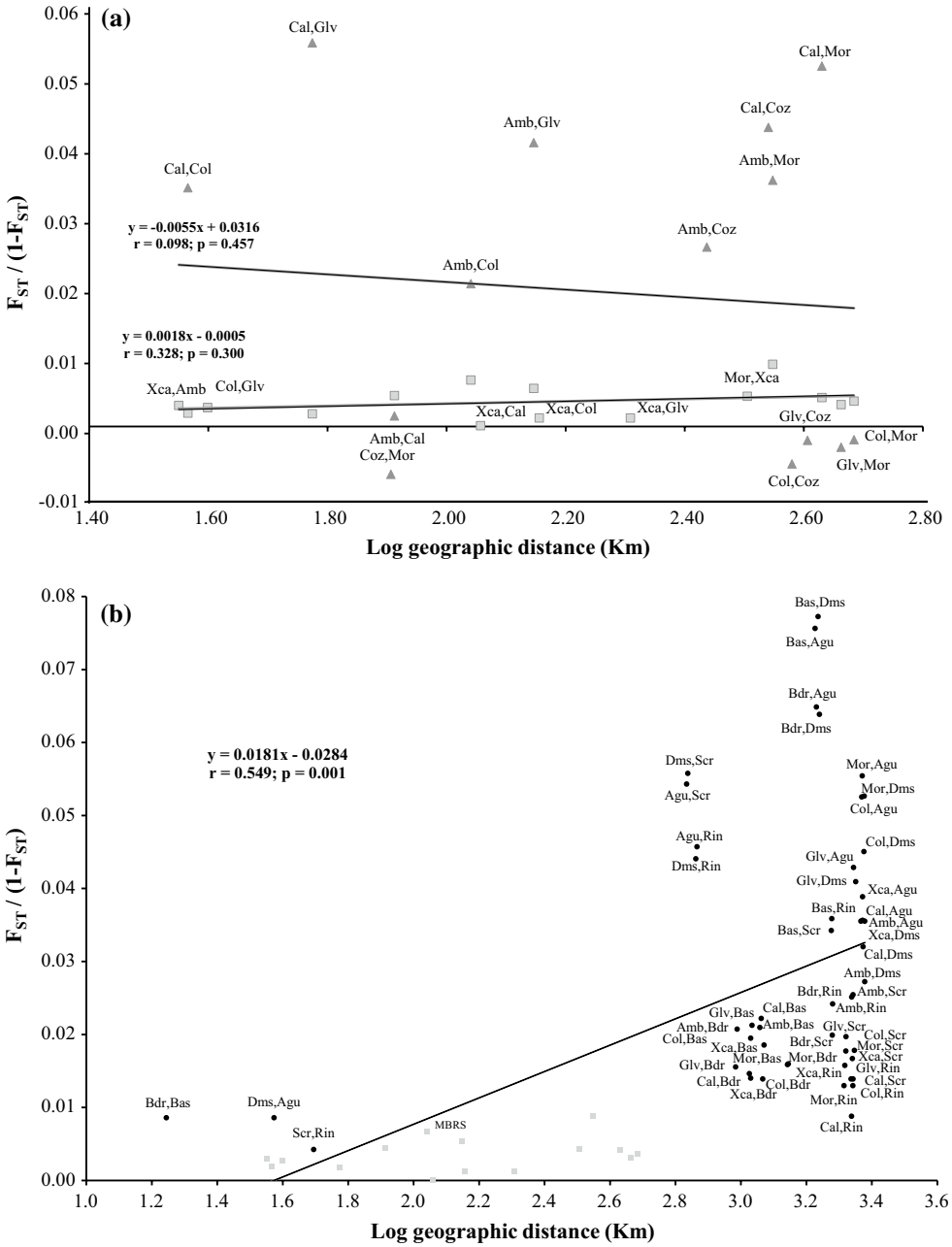

Fig. 2 Mantel tests along the Mesoamerican Barrier Reef System (MBRS) for *O. faveolata* (triangles) and *A. palmata* (squares) (**a**), *A. palmata* at larger scale (>1,000 km) (**b**). *Light gray squares* illustrate pairwise comparison between populations from the MBRS, detailed labels for these data points are shown in *panel* **a**. *Black circles* represent the rest of *A. palmata* populations

samples from Venezuela also showed three main groupings (Fig. 3d). These findings, both from the PCoA based on F_{ST} measures and the Bayesian cluster analysis, corroborated that the populations of *A. palmata* are grouped in four clusters.

AMOVA of *F*-statistics partitioned the majority of the genetic variance (96.77 %; Table 5) to variation within populations. However, remaining variation among regions and among populations within regions was also significant, but only explaining 2.75 and 0.48 % of the variance, respectively (Table 5).

Discussion

The major findings of this study are as follows: (1) the majority of *O. faveolata* and *A. palmata* populations had high genetic diversity and low clonality; (2) both species showed similar patterns of population structure within the MBRS, with low-to-moderate differentiation among populations; (3) at a larger spatial scale (i.e., Caribbean-wide), *A. palmata* populations were grouped into four interconnected subpopulations: MBRS, Panama, Puerto Rico and Venezuela.

Table 3 Pairwise F_{ST} values for (a) *O. faveolata* MBRS, (b) Caribbean-wide *A. palmata* populations

	Mor	Coz	Cal	Amb	Col						
(a)											
Coz	−0.007										
Cal	0.049*	0.041									
Amb	0.034*	0.025	0.001								
Col	−0.003	−0.006	0.033*	0.020*							
Glv	−0.002	−0.002	0.052*	0.039*	0.002						
	Mor	Xca	Amb	Cal	Glv	Col	Bdr	Bas	Dms	Agu	Scr
(b)											
Xca	*0.004*										
Amb	*0.009**	*0.003*									
Cal	*0.004*	*0.000*	*0.004*								
Glv	*0.004**	*0.001*	*0.005**	*0.002*							
Col	*0.003**	*0.001*	*0.007**	*0.002*	*0.003**						
Bdr	0.016*	0.014*	0.021*	0.014*	0.015*	0.014*					
Bas	0.016*	0.018*	0.022*	0.021*	0.020*	0.019*	0.009*				
Dms	0.050*	0.034*	0.027*	0.031*	0.039*	0.043*	0.060*	0.072*			
Agu	0.053	0.037*	0.034*	0.034*	0.041*	0.050*	0.061*	0.070*	0.009*		
Scr	0.017*	0.016*	0.025*	0.013*	0.019*	0.018*	0.020*	0.033*	0.053*	0.052*	
Rin	0.013*	0.014*	0.025*	0.009*	0.016*	0.014*	0.024*	0.035*	0.044*	0.042*	0.004

In italics, MBRS populations

* Significant *P* values obtained after 300 for *O. faveolata* and 1,320 permutations for *A. palmata;* indicative adjusted nominal level (5 %) for multiple comparisons is: 0.003333 for *O. faveolata* and 0.000758 for *A. palmata*. Abbreviations are as in Table 1

Low clonality and high genetic diversity in *O. faveolata* and *A. palmata*

The contribution of sexual and asexual reproduction to coral population dynamics can be highly variable (Harrison and Wallace 1990), and environmental factors may influence their relative importance (Highsmith 1982; McFadden 1997; Coffroth and Lasker 1998; Lirman 2000). For example, clonality in *Pocillopora damicornis* varies among populations from almost no clonality to very high levels (Adjeroud et al. 2014 and references therein).

The low proportion of clones (%) among colonies that were at least >5 m apart (Table 1) was a consistent result across most populations of both *O. faveolata* and *A. palmata*, suggesting that sexual reproduction has contributed significantly to their demographic structure at our study sites. Although Puerto Rico and Panama populations had a lower proportion of unique *A. palmata* haplotypes ($N_g/N = 0.66 \pm 0.01$ and $N_g/N = 0.74 \pm 0.01$, respectively; Table 1), these populations still had a large number of genets compared to Florida Keys populations of *A. palmata*, for example, where high clonality has been frequently observed (e.g., Baums et al. 2005b, 2006). Furthermore, Baums et al. (2006) found that the western Caribbean was genotypically depauperate ($N_g/N = 0.43 \pm 0.31$) while the eastern Caribbean was genotypically rich ($N_g/N = 0.64 \pm 0.17$). In the present study such pattern was not found, all populations had a large proportion of unique haplotypes. These contrasting results are likely due to the difference in the sampling size (larger in our study; $n = 39$–115; Table 1), and/or in the sampling scale (here colonies were >5 m apart over an area of 1 km^2). In particular, Baums et al. (2006) sampled 15–24 individuals per population of *A. palmata* which only allows for characterization of <50 % of the allele richness in neutral nuclear loci in this species (Shearer et al. 2009). Furthermore, they reported high clonality among colonies within a 5-m-radius plot, and further increasing this radius to 10 and 15 m did not significantly increase the number of genets.

Vollmer and Palumbi (2007) reported similar results to those found in this study for the congener *A. cervicornis*, stressing that recent estimates of genetic diversity for this species parallels diversity estimates prior to massive mortality events (Neigel and Avise 1983; Vollmer and Palumbi 2007). In the particular case of *A. palmata*, sexual reproduction has contributed significantly to the demographic structure found at our sites and those reported in other studies (Zubillaga et al. 2008). However, asexual reproduction can be more prevalent in *A. palmata* at some sites

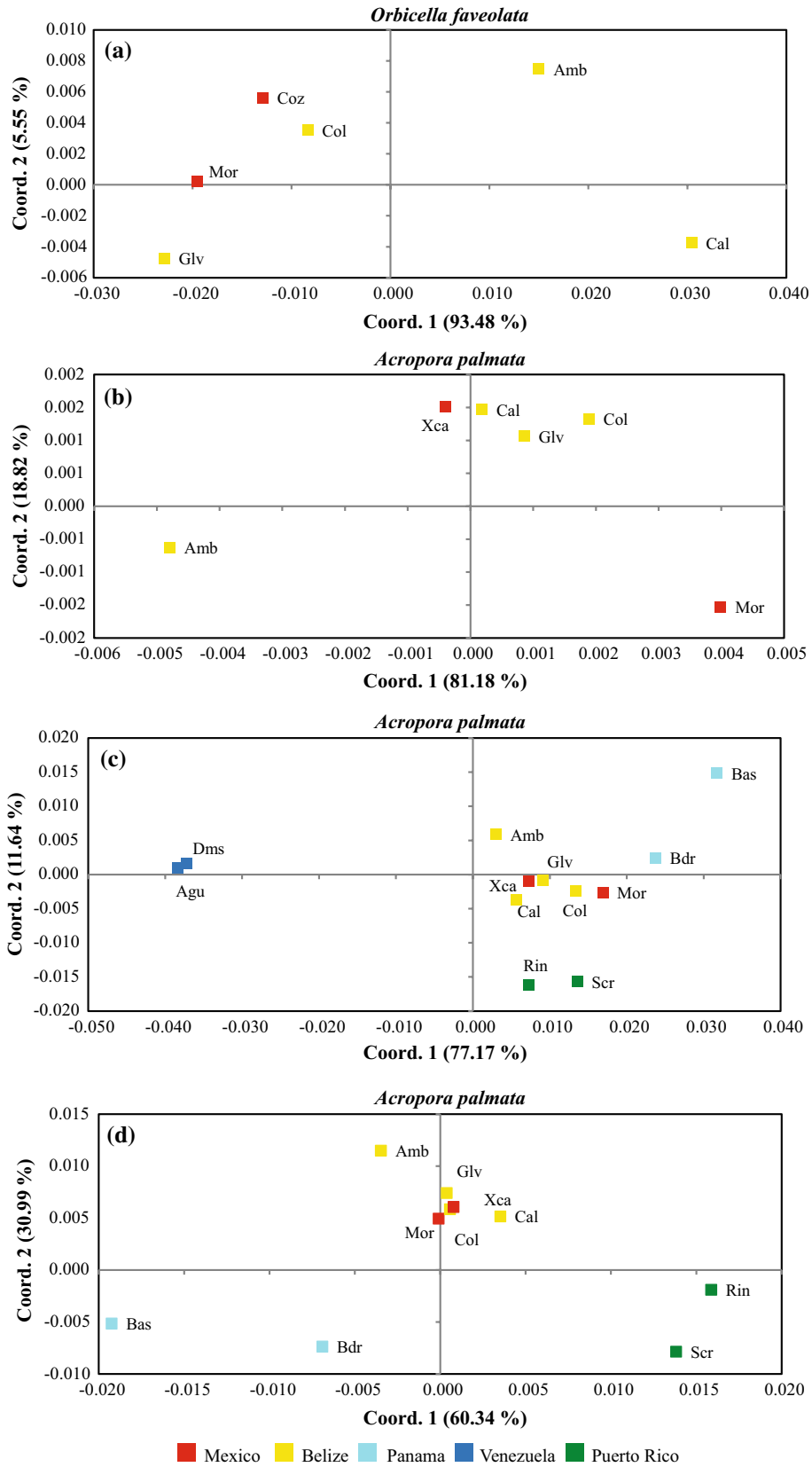

Fig. 3 PCoA of pairwise FST estimates among populations of *O faveolata* (**a**), and *A. palmata* (**b**) at regional scale (MBRS), *A. palmata* at large scale (>1,000 km) (**c**), and *A. palmata* Puerto Rico, MBRS and Panama cluster (**d**). Percentages indicate the proportion of variation attributed to each coordinate. Abbreviations are as in Table 1

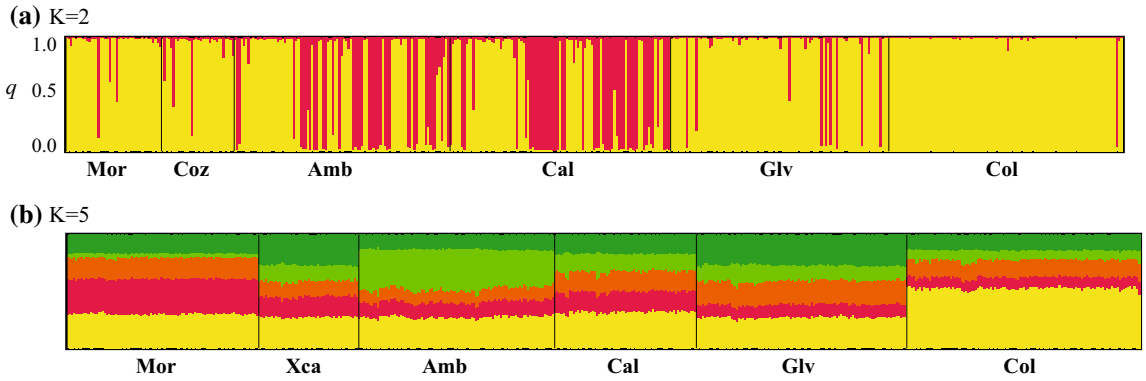

Fig. 4 Number of clusters (K) and group membership coefficient (q) calculated in Structure 2.3.3 for *O. faveolata* (**a**) and *A. palmata* (**b**), using LOCPRIOR. ΔK (Evanno et al. 2005), plots of the maximal value of the probability of the data Ln $Pr(X|K)$, against a range of K and analysis of alternative solutions available in the Online Resources 5. Abbreviations are as in Table 1

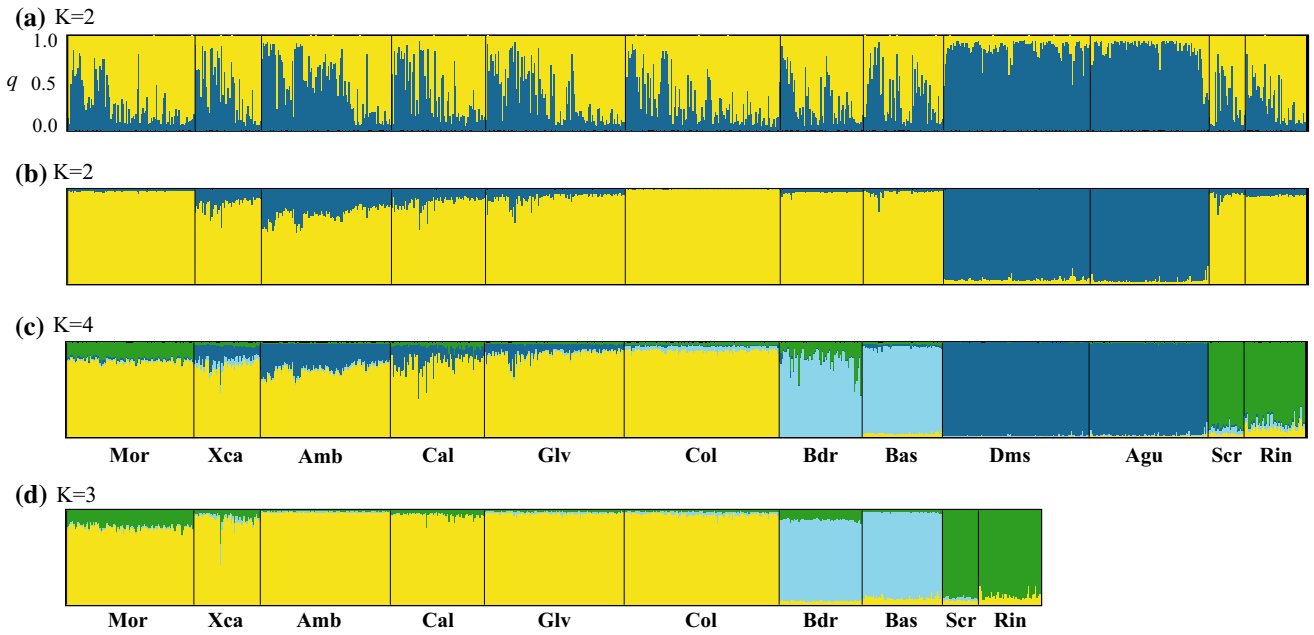

Fig. 5 Number of clusters (K) and group membership coefficient (q) calculated in Structure 2.3.3 for all *A. palmata* sampled population using the standard method (not using location as a prior) (**a**), using LOCPRIOR (**b**), alternative solution $K = 4$ using LOCPRIOR (**c**), sub-clustering eliminating Venezuela, using LOCPRIOR (**d**). ΔK (Evanno et al. 2005) and plots of the maximal value of the probability of the data Ln $Pr(X|K)$, against a range of K are available in the Online Resources 6. Abbreviations are as in Table 1

and result in patches of closely spaced colonies of the same clone (Baums et al. 2005b, 2006).

Orbicella faveolata reproduces mainly sexually (e.g., Knowlton et al. 1997; Sánchez et al. 1999; Villinski 2003; Szmant and Miller unpubl data), and low clonality has been reported (Severance and Karl 2006). In this study, few *O. faveolata* colonies that were at least 5 m apart had identical multilocus genotypes (Table 1). This result was expected given that the experimental design aimed to avoid clonemates. However, asexual reproduction in *O. faveolata* can occur by breakage of overhanging skirts of large colonies (Highsmith 1982), or by partial mortality. The closely related species *O. annularis* consists of clusters of columns can also propagate asexually due to disturbances like hurricanes (Highsmith 1982; Severance and Karl 2006; Foster et al. 2007, 2013). Detailed studies on the contribution of asexual reproduction in *O. faveolata* are needed at smaller scales given that in massive corals, fragmented pieces will recruit adjacent to the donor colony.

Overall, high genetic diversity was observed for both species (Table 2; Online Resource 6) implying adequate gene flow to maintain diversity against loss of genotypes

Table 4 Hierarchical analysis of molecular variance (AMOVA) for *O. faveolata* and *A. palmata* multilocus microsatellite variation among regions (guided by the final number of ancestral clusters, *K*; see text for details), among populations within regions and within populations

Source	*O. faveolata*				*A. palmata*			
	df	SSquares	%	*F*	*df*	SSquares	%	*F*
Among regions	1	26.53	3.95	0.039	4	12.78	0.37	0.004
Among populations within regions	4	1.47	0	−0.005	1	1.18	0.01	0.0001
Within populations	924	1,325.20	96.55	0.034*	1,024	1,834.56	99.62	0.004*
Total	929	1,353.20			1,029	1,849.16		

df = degrees of freedom, % = the proportion of the total variation partitioned to each hierarchical level, *F* = fixation indices

* Significant *P* values obtained after 1,023 permutations, $\alpha = 0.0001$

Table 5 Hierarchical analysis of molecular variance (AMOVA) for *A. palmata* multilocus microsatellite variation among regions (MBRS, Panama, Venezuela and Puerto Rico), among populations within regions and within populations

Source	*df*	SSquares	%	*F*
Among regions	3	62.085	2.75	0.027*
Among populations within regions	8	24.514	0.48	0.005*
Within populations	1,780	3,109.714	96.77	0.032*
Total	1,791	3,196.312		

df = degrees of freedom, % = the proportion of the total variation partitioned to each hierarchical level, *F* = fixation indices

* Significant *P* values obtained after 1,023 permutations, $\alpha = 0.0001$

during recent coral population declines. The maintenance of high levels of genetic diversity can enhance the capacity for population adaptation and resilience (Frankham 2005). With reduced gene flow, genetic diversity within a population may decline over time as unfavorable changes in the environment (e.g., seawater warming events that results in bleaching, disease and coral death) result in the rapid loss of genetic diversity, and loss in the ability to adapt to additional perturbations (van Oppen and Gates 2006). There is increasing evidence of genotype-specific tolerance to changes in environmental conditions, including bleaching and disease resistance (Altizer et al. 2003; Coles and Brown 2003; D'Croz and Maté 2004; Maynard et al. 2008; Baums et al. 2013). Populations with a high influx of larvae from a single genetically diverse source, or from multiple larval sources, may have a higher probability of acquiring these beneficial alleles into their genetic pool.

For both species, populations from Col (Belize) had the lowest allelic richness and *O. faveolata* populations from Glv (Belize) showed the lowest allelic richness in three out of the five examined loci (Online Resource 6), although this was not observed in *A. palmata* at this site. Total coral cover on Glover's Reef decreased from 80 to 13 % between 1971 and 1999 (McField et al. 2008) and could be responsible for the loss of alleles. Alternatively, but less likely, populations in these two sites (Col and Glv) were either less genetically diverse before the coral decline, and/or colonies carrying some of the missing alleles had higher rates of mortality. Unfortunately, there are no measurements of genetic diversity prior to the population declines that have occurred over the last 30–40 years in the Caribbean.

Large population reductions often contribute to decreases in genetic diversity through bottleneck effects and genetic drift (Nei et al. 1975; Cornuet and Luikart 1996; Leberg 2002). However, the relative importance of these driving forces can be small in the observed genetic diversity of these two coral species, particularly for *O. faveolata*, which have suffered relatively recent declines compared with its long life span, low recruitment and slow growth rates (see below for further discussion).

Orbicella faveolata and *A. palmata* population structure within the MBRS

The most significant finding of this study is that both species showed similar patterns of population structure within the MBRS, with low, yet significant population structure. However, Amb (Belize) and Cal (Belize) for *O. faveolata* and Amb (Belize) and Mor (Mexico) for *A. palmata* differed from all other MBRS populations (low but significant F_{ST}). Furthermore, differentiation among *O. faveolata* populations seemed greater than those for *A. palmata* (Fig. 2a).

Interpreting the biological relevance of low, but statistically significant F_{ST} values is often a challenge, especially in marine populations that often have notoriously low signals of population differentiation (Waples 1998). The higher mutation rates of microsatellites result in a high degree of polymorphism that can deflate significantly F_{ST} values, and for multiallelic markers, the expected value under complete differentiation will not be one (Reviewed in Balloux and Lugon-Moulin 2002; Meirmans and Hedrick 2011). The maximum F_{ST} value will be determined by the amount of within-population diversity (Charlesworth 1998; Hedrick 1999). Here, the H_e (Expected heterozygosity) was high for both species (Table 2), suggesting that population

differentiation may be higher than indicated by the F_{ST} values.

Both coral species have similar reproductive strategies (e.g., broadcast spawners during synchronous events in the summer), which could serve as an explanation for their similar population structure patterns along the MBRS. However, their larval development times differ by a factor of two. The majority (72 %) of *A. palmata* larvae settle after 8–9 days (Zubillaga 2010); however, larvae can remain competent in the water column for up to 3 weeks (Szmant unpubl data). Larvae of *O. faveolata* are generally competent to settle in only 3–4 days (Szmant and Miller unpubl data), but have been observed to remain competent as long as 10–20 days under laboratory conditions (Zubillaga and Szmant unpubl data). Larvae of both species can swim (<1.5 mm s^{-1} for *O. faveolata*, Vermeij et al. 2006; 0.10 ± 0.09 mm s^{-1} SD for *A. palmata*, Baums et al. 2013), but these speeds are too slow for them to swim against the current. Thus, the longer time to settlement (8–9 days for *A. palmata* vs. 3–4 days for *O. faveolata*) might have been expected to result in greater dispersal ability and less population differentiation for *A. palmata* than for *O. faveolata*.

The two species studied here, as well other scleractinian species, are typical *K*-selected species characterized by very long-lived individuals, and populations with historically low levels of recruitment (Smith 1992; Miller et al. 2000). For *O. faveolata* and *A. palmata,* the populations sampled in this study were composed of mid-size adults (20–100 cm maximum diameter) and adults (>100 cm maximum diameter). Large adults recruited long before the recent widespread degradation of Caribbean coral reefs. Thus, the population genetic structure patterns identified in this study and in other *K*-selected scleractinian species may reflect patterns of historic connectivity prior to recent reef declines if only large adults were included, although *Orbicella* species exhibits much slower growth rates than the *Acropora* species (Gladfelter et al. 1978). In order to estimate current patterns of gene flow, collection of juveniles (non-remnant colonies of <5 cm maximum diameter) was intended, but not enough recruits were found for population genetic analysis.

In this study, the majority of *O. faveolata* colonies from Mor (Mexico), Glv and Col (Belize) were >100 cm in length (i.e., maximum diameter; data not shown). However, for Amb, Cal (Belize) and Coz (Mexico), the majority of sampled colonies were mid-size adults (20–100 cm maximum diameter; data not shown). For *A. palmata,* the distribution of size classes was similar across the populations, and most colonies were 50–100 cm in length (i.e., maximum diameter; data not shown). In the case of *O. faveolata,* this difference in the distribution of size classes could help explain the observed population genetic structure. Populations from Mor (Mexico), Glv and Col (Belize) are composed of large, thus, older colonies and could be reflecting historic patterns of population structure, whereas Amb and Cal (Belize), where colonies are smaller, may be reflecting more recent population structure. Total or partial colony mortality could reduce fertilization by increasing the distance between colonies or decreasing fecundity, which will result in a reduction in fertilization success and larval production. With a decreased larval supply, local recruitment and dispersal to non-local populations may be reduced, decreasing gene flow between once-connected populations.

Lack of correlation between genetic and geographic distance among populations where geographically distant populations are genetically more similar than geographically close ones has also been reported in the coral species *Pocillopora damicornis* on reefs in east Africa (Souter et al. 2009), the sea urchin populations in southeastern Australia and New Zealand (Banks et al. 2007) and the bicolor damselfish (*Stegastes partitus*) in the MBRS (Hepburn et al. 2009). This pattern could indicate that other biological factors (e.g., natural selection) (Cowen et al. 2006; Purcell et al. 2006; Selkoe et al. 2006; Gerlach et al. 2007; Jones et al. 2009; Bongaerts et al. 2010), other life history traits like temporal variation in fecundity (Hughes et al. 2000, 2002) or larval mortality (reviewed in Sponaugle et al. 2002) or/and oceanographic conditions (Cowen et al. 2000; Baums et al. 2006; Butler et al. 2011; Foster et al. 2012) could be influencing population structure. The lack of relationship between genetic and geographic distances observed in *O. faveolata* and *A. palmata* within the MBRS supports the growing notion that although larval dispersal is necessary for connectivity among coral populations, dispersal capabilities and distance between populations are not adequate predictors of genetic structure and realized biological connectivity.

Sub-structuring within the MBRS has also being reported for *Orbicella annularis*, a sister taxa of *O. faveolata* (Foster et al. 2012). Populations of *O. annularis* from Belize formed a cluster with the Bahamas, Cuba and the Caiman Islands, and Honduras was grouped with Jamaica, Nicaragua, Colombia, Puerto Rico, British Virgin Islands and Dominican Republic. The authors attributed this population structure between Belize and Honduras to an ephemeral salinity gradient that could act as a temporary barrier of low salinity that may reduce the survival of larvae moving from Honduras to Belize. Even though environmental stress (e.g., reduced salinity) has been demonstrated to affect *O. faveolata*'s larval behavior, survival and settlement patterns (Vermeij et al. 2006), greater population differentiation would have been observed along the MBRS because reefs along the MBRS, including offshore atolls, are under the influence of terrestrial runoff on a seasonal basis (Paris and Cherubin 2008; Chérubin et al. 2008; Soto

et al. 2009). Furthermore, strong population differentiation for *O. annularis* but low for *O. faveolata* has been reported for Puerto Rico, the lower Florida Keys and the Yucatan Peninsula (Severance and Karl 2006), suggesting that other evolutionary or ecological factors are contributing to the observed population structure patterns (Severance and Karl 2006).

Genetic population structure of *Acropora palmata* at regional and Caribbean-wide spatial scales

Patterns of population structure in *A. palmata* over Caribbean basin-wide spatial scales were consistent with other Caribbean-wide studies of this coral species corroborating that *A. palmata* does not constitute a single, interbreeding population throughout its geographic range (e.g., Baums et al. 2005a). Baums et al. (2005a) concluded that populations of this species are divided into two different biogeographic regions (i.e., eastern and western Caribbean). Our results suggest that *A. palmata* is further subdivided into four subregions (the MBRS, Puerto Rico, Venezuela and Panama). Furthermore, the overall observed genetic structure of *A. palmata* was explained by the isolation-by-distance model, and it follows the typical pattern characterized by small slopes and large scattering (Puebla et al. 2012) supporting the idea that *A. palmata* has limited dispersal at the Caribbean-wide spatial scale. Low but significant population pairwise F_{ST} values suggest that some restricted gene flow exists or may have existed among regions. However, this gene flow may not indicate long-distance dispersal at ecological timescales or demographic connectivity (Puebla et al. 2012).

The existence of regional subdivision has also been found in *O. annularis* (Foster et al. 2012) and *Gorgonia ventalina* (Andras et al. 2013). However, the subregions are defined by different populations of the same species. For example, Andras et al. (2013) found that populations of *G. ventalina* from Puerto Rico are different from the ones in Panama and the MBRS, similar to the pattern reported here for *A. palmata*. Additionally, they found no subdivision between Panama and the MBRS. *Orbicella annularis* is genetically differentiated into three regions: eastern Caribbean (Lesser Antilles, Venezuela and Curacao), western Caribbean (the Bahamas, Cuba, Belize and Cayman Islands) and central Caribbean (Jamaica, Honduras, Nicaragua, Colombia, Puerto Rico, British Virgin Islands and Dominican Republic) (Foster et al. 2012).

The concept of the existence of regional subdivisions across the Caribbean introduced by Robins (1971) and Briggs (1974) is controversial. For instance, studies conducted with populations of the bicolor damselfish, *Stegastes partitus*, which has a larval duration of ca. 20–40 days (Robertson et al. 1988; Wellington and Victor 1989), did not exhibit marked genetic structure across the Caribbean ($F_{ST} = 0.0031$, $R_{ST} = 0.003$, Hepburn et al. 2009; Sala et al. 2010, respectively). Díaz-Ferguson et al. (2010) did not find that the population structure of the gastropod *Cittarium pica* in the Caribbean differed between the eastern and western Caribbean, but did report that populations from Bonaire (close to Venezuela) were isolated from the rest of the Caribbean. Other studies of fish, soft corals and sponges have found a variety of levels of gene flow among populations (Duffy 1993; Shulman and Bermingham 1995; Rocha et al. 2002; Taylor and Hellberg 2003; Gutiérrez-Rodríguez and Lasker 2004; Bowen et al. 2006; Ospina-Guerrero et al. 2008) or even a lack of genetic structure among many Caribbean taxa (e.g., queen conch; Mitton et al. 1989, sea urchins; Lessios et al. 1999, 2001, 2003; *Montastraea cavernosa*; Nunes et al. 2009; Goodbody-Gringley et al. 2011). Furthermore, the existence of the divide between the eastern and western Caribbean in the southern Caribbean is not clear-cut. Baums et al. (2005a) placed Venezuela in the eastern Caribbean. However, Galindo et al. (2006), using various deterministic and stochastic oceanographic models, found differentiation between eastern and western Caribbean *A. cervicornis* populations and placed Venezuela in the western Caribbean.

The high F_{ST} values observed between populations from Panama and Venezuela may be the result of geographic distance combined with the circular gyre of the Caribbean current in the Colombian basin, likely preventing larval dispersal from Venezuela to Panama. This divide was also found for *O. annularis* (Foster et al. 2012), and the authors attributed this result to a barrier formed by a plume of low salinity run-off from the Magdalena River (Colombia) (Restrepo and Kjerfve 2000). Furthermore, small but significant pairwise F_{ST} values were found between population Agu and Dms (Venezuela), which are 5 km apart, and between Bas and Bdr (Panama), which are 16 km apart ($F_{ST} = 0.009$, $P = 0.00076$ both cases). Even though the null hypothesis of panmixia between these populations is rejected, the F_{ST} values are too low to conclude that these populations are genetically differentiated.

Management considerations

Managers should be cautious when interpreting studies of population genetic structure for use as criteria in developing management strategies. The rate of recruitment of foreign larvae required to achieve genetic connectivity is significantly less than the rate required to achieve meaningful demographic connectivity (recruitment sufficient to repopulate a deteriorating coral population). This is particularly true with long-lived corals such as *A. palmata* and *O. faveolata* whose current genetic structure was determined by an accumulation of (possibly infrequent) recruitment events over decades or centuries.

The populations sampled in this and other studies were mid-sized adults and adults that recruited long before the recent widespread degradation of Caribbean coral reefs. Thus, the Caribbean-wide population structure patterns identified here and in other studies may not reflect patterns of demographic connectivity occurring among contemporary reefs, but rather historic connectivity prior to recent reef decline. With this caveat in mind, these data can be useful for management consideration. Firstly, *A. palmata* is divided between four regions. While the low F_{ST} values suggest some historic gene flow, significant differentiation was found so that this flow may be restricted or not be of ecological significance. Thus, these subregions should be considered as independent Conservation Units (Moritz 1994).

Furthermore, in previous studies of population structure of *O. faveolata* across large geographic scales (Caribbean, Severance and Karl 2006; Baums et al. 2010) and along the Florida Reef Track (Baums et al. 2010), panmixia among populations was observed (Baums et al. 2010). In contrast, our study shows low-to-moderate population structure within the MBRS for both *O. faveolata* and *A. palmata*. Thus, the management strategies for reefs like Amb (Belize) and other populations where gene flow is restricted may differ from strategies for reefs that may expect recruitment of foreign larvae to replenish declining populations.

Lastly, most *A. palmata* and *O. faveolata* populations in this study were genetically diverse despite general widespread coral mortality throughout the Caribbean for the past three decades. These results suggest that conservation efforts for these coral species need to be conducted on both local and regional levels with the active participation of multiple countries. A greater understanding of the factors that influence the high larval mortality and subsequent recruitment failure experienced by these species is needed to establish an effective management strategy.

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