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Distinct Phenotypes Associated with Mangrove and Lagoon Habitats in Two Widespread Caribbean Corals, *Porites astreoides* and *Porites divaricata*

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Abstract. As coral reefs experience dramatic declines in coral cover throughout the tropics, there is an urgent need to understand the role that non-reef habitats, such as mangroves, play in the ecological niche of corals. Mangrove habitats present a challenge to reef-dwelling corals because they can differ dramatically from adjacent reef habitats with respect to key environmental parameters, such as light. Because variation in light within reef habitats is known to drive intraspecific differences in coral phenotype, we hypothesized that coral species that can exploit both reef and mangrove habitats will exhibit predictable differences in phenotypes between habitats. To investigate how intraspecific variation, driven by either local adaptation or phenotypic plasticity, might enable particular coral species to exploit these two qualitatively different habitat types, we compared the phenotypes of two widespread Caribbean corals, *Porites divaricata* and *Porites astreoides*, in mangrove *versus* lagoon habitats on Turneffe Atoll, Belize. We document significant differences in colony size, color, structural complexity, and corallite morphology between habitats. In every instance, the phenotypic differences between mangrove prop root and lagoon corals exhibited consistent trends in both *P. divaricata* and *P. astreoides*. We believe this study is the first to document intraspecific phenotypic diversity in corals occupying mangrove prop root *versus* lagoonal patch reef habitats. A difference in the capacity to adopt an alternative phenotype that is well suited to the mangrove habitat may explain why some reef coral species can exploit mangroves, while others cannot.

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Introduction

Globally, coral reefs are declining at an alarming rate as a result of the effects of climate change, especially rising sea surface temperatures and ocean acidification (Hughes *et al.*, 2017), as well as a myriad of local anthropogenic stressors (Ban *et al.*, 2014). However, reefs are not the only habitat in which corals can live. Many coral species are habitat generalists that can thrive in a multitude of different environments in addition to coral reefs, including seagrass beds (Camp *et al.*, 2016; Lohr *et al.*, 2017) and mangroves. With respect to mangroves, corals have been reported growing directly on mangrove prop roots (Rogers and Herlan, 2012; Yates *et al.*, 2014; Hernández Fernández, 2015; Rogers, 2017; Bengtsson *et al.*, 2019; Kellogg *et al.*, 2020), on the benthos under the shade of the mangrove canopy (Rogers and Herlan, 2012; Yates *et al.*, 2014; Rogers, 2017; Kellogg *et al.*, 2020), and in lagoonal habits bounded by mangroves, although not shaded by the mangrove canopy (Rogers and Herlan, 2012; Yates *et al.*, 2014; Camp *et al.*, 2016, 2019; Rogers, 2017). About half of the approximately 75 coral species that occur on Caribbean reefs also occur in mangrove habitats (Rogers and Herlan, 2012; Yates *et al.*, 2014; Hernández Fernández, 2015; Rogers, 2017; Bengtsson *et al.*, 2019; Kellogg *et al.*, 2020).

The ability to live and reproduce in a range of habitats or under a multitude of conditions could substantially increase species' survival rates in this period of rapid environmental change and increased environmental variability. Indeed, corals that do not rely exclusively on reef habitats have been shown to be less vulnerable to environmental change (Carpenter *et al.*, 2008). As a result, in many locations throughout the Caribbean, species that were competitively dominant during prior periods of environmental stability are being replaced

by "weedy" species that can survive across a range of habitats (Darling *et al.*, 2012, 2013). For example, the iconic Caribbean branching corals *Acropora cervicornis* (Lamarck, 1816) and *Acropora palmata* (Lamarck, 1816) were able to grow rapidly and outcompete other corals under the relatively stable conditions that persisted on Caribbean reefs for most of the past few thousand years (Aronson *et al.*, 2002; Darling *et al.*, 2012). However, in recent decades, these acroporids have suffered severe declines (Aronson and Precht, 2001; Precht *et al.*, 2002), while slower-growing stress-tolerant massive corals (*e.g.*, *Orbicella* spp.) and rapidly recruiting weedy corals (*e.g.*, *Porites* spp.) have increased in prevalence (Edmunds and Carpenter, 2001; Gardner *et al.*, 2003; Green *et al.*, 2008). Weedy corals have been found to exhibit greater intraspecific variation in phenotypic traits than corals with other life-history strategies, such as competitively dominant species, stress-tolerant species, and generalists (Darling *et al.*, 2012). Thus, the fact that weedy corals are increasing in relative abundance on reefs could be due, in large part, to this intraspecific variation; however, there could be several other contributors to their success, such as that they predominately exhibit a brooding reproductive mode and high fecundity (Darling *et al.*, 2012). Consequently, the future composition of coral assemblages in the Caribbean and elsewhere may depend, in part, on how increasing environmental variation affects the physiology, morphology, and fitness of these habitat generalists.

One way to investigate how environmental variation affects coral phenotypes is to compare the same coral species across an environmental gradient. Resulting differences in phenotype may be attributed to phenotypic plasticity (environmentally induced), genotype, or a combination of the two (Todd, 2008). Environmental variation across sites has been associated with changes in many phenotypic traits in corals, including colony form (Muko *et al.*, 2000), branching pattern (Bruno and Edmunds, 1998; Kaandorp, 1999; Doszpot *et al.*, 2019), corallite architecture (Todd *et al.*, 2004; Studivan *et al.*, 2019), and color (Gleason, 1993, 1998). The observed phenotypic variation has been associated with variation in a number of environmental variables that are known to differ between mangrove and reef habitats, such as light (Ow and Todd, 2010), flow (Lesser *et al.*, 1994), sedimentation (Gleason, 1998), and nutrients (Bongiorni *et al.*, 2003a, b).

To investigate how intraspecific variation, driven by either genetic variation or phenotypic plasticity, might enable corals to exploit two qualitatively different habitat types, we compared the phenotypes of two widespread Caribbean corals, *Porites divaricata* Le Sueur, 1820 and *Porites astreoides* Lamarck, 1816, in mangrove *versus* lagoon habitats on Turneffe Atoll, Belize (Fig. 1). These two weedy corals can be found in a wide variety of habitats, including seagrass beds, mangrove forests, and lagoonal patch reefs, as well as across distinct reef zones (Veron, 2000; Hernández Fernández, 2015; Camp *et al.*, 2016; Rogers, 2017; Bengtsson *et al.*, 2019). The mustard hill coral, *P. astreoides*, exists as a massive, encrusting, or plating form, with colors ranging from bright yellow to medium gray to dark brown (Fig. 2; Veron, 2000). The thin finger coral, *P. divaricata*, is a branching coral that can vary greatly in overall shape, number, and density of branch tips and in color (Fig. 3). *Porites divaricata* belongs to a complex of three closely related Caribbean branching corals, along with *Porites porites* (Pallas, 1766) and *Porites furcata* Lamarck, 1816. In the field, these morphologically similar corals are distinguished primarily by branch diameter and habitat preference. *Porites divaricata* exhibits the thinnest branches and a preference for lee habitats, such as mangrove and lagoon (Jameson, 1997; Prada *et al.*, 2014). In selecting specimens for the current study, we chose colonies with the thinnest branch diameters in both mangrove and lagoon habitats (Table 1). However, there is debate in the literature as to whether these three Caribbean branching *Porites* represent a single morphologically variable species, rather than three discrete species. We consider the potential ramifications of alternative taxonomic relationships for the conclusions of this study in the Discussion.

While previous studies have explored the phenotypic variation of *P. astreoides* (Gleason, 1993) and *P. divaricata* (Bengtsson *et al.*, 2019) within habitat types, this study characterizes differences between coral species inhabiting mangrove prop root and shallow lagoon habitats (not associated with mangroves). Given that our mangrove and lagoon habitats differ in key environmental parameters, including temperature and light, we hypothesized that colonies from the two study locations would exhibit consistent and predictable differences in phenotype. Specifically, we expected that corals in the mangrove sites would exhibit traits associated with lower light levels, such as darker coloration (Gleason, 1993) and distinct corallite architecture (Ow and Todd, 2010; Soto *et al.*, 2018). We also expected colony morphology (*i.e.*, colony size) to differ because in the mangroves, colonies are attached to an approximately vertical substrate (prop roots of the red mangrove, *Rhizophora mangle* (L.)), while in the lagoon, colonies are attached to an approximately horizontal substrate. Over 2 years of sampling, we characterized multiple phenotypic traits of 249 coral colonies and found significant differences in colony size, structural complexity, color, and form between corals inhabiting mangrove and lagoon habitats.

Materials and Methods

Corals were characterized at three sites on Turneffe Atoll, Belize: a shallow lagoon site not directly adjacent to mangroves and two mangrove-lined channels (Fig. 1). Turneffe Atoll, located about 32 km off of the coast of Belize, is one of only 4 atolls in the Western Hemisphere and is the largest of the 3 Belize atolls, with an area of about 531 km^2 (Stoddart, 1962). Unique in the Belizean atolls, Turneffe is dominated

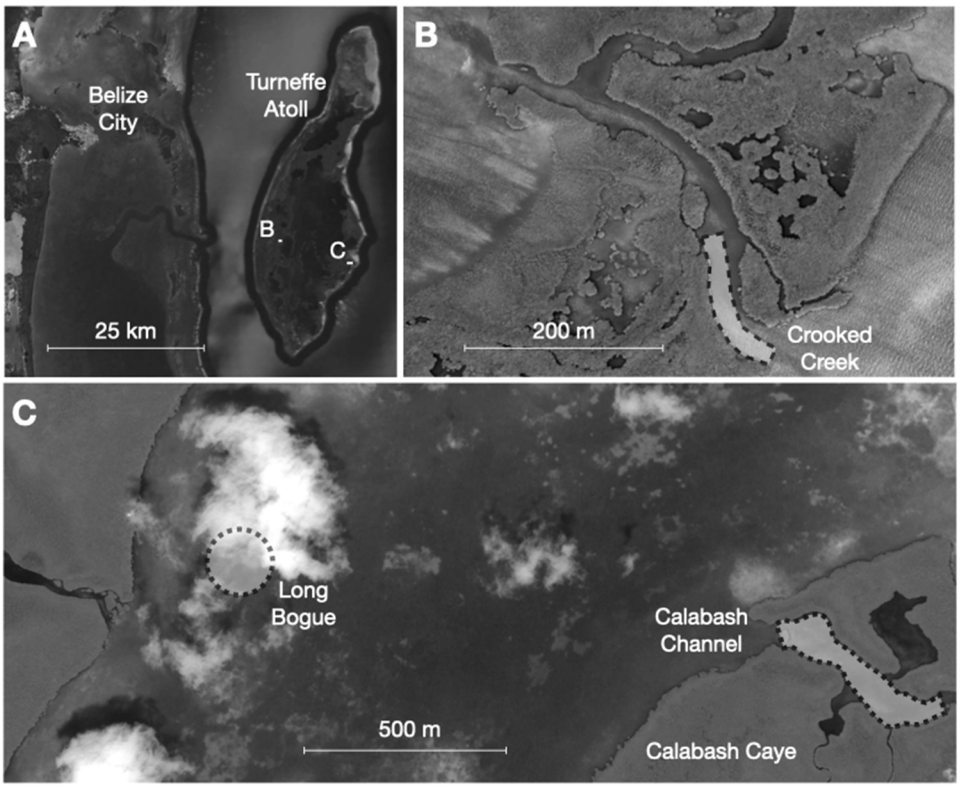

Figure 1. Location of study sites on Turneffe Atoll, Belize. (A) Turneffe Atoll. (B) Crooked Creek. Light gray region encompassed by dashed lines indicates where *Porites divaricata* and *Porites astreoides* colonies were sampled growing on mangrove prop roots. The approximate center of the shoreline of Crooked Creek is 17°19′45.78″ N, 87°55′6.35″ W. (C) Lagoon patch reef site at Long Bogue and mangrove site at Calabash Channel. The approximate center of the Long Bogue site, where colonies were sampled (gray shading), is located at 17°17′25.84″ N, 87°49′42.34″ W. The approximate center of the Calabash Channel site, where corals were sampled growing on mangrove prop roots (gray shading), is located at 17°17′16.23″ N, 87°48′48.20″ W. The image is dated August 26, 2005, and was obtained using Google Earth Pro (ver. 7.3.2.5776). Image © 2020 Maxar Technologies.

by mangroves. *Rhizophora mangle* L. is practically ubiquitous at the water's edge, and lesser amounts of *Avicennia germinans* (L.) Stearn. and *Laguncularia racemosa* (L.) C.F. Gaertn. grow in the interior of the hundreds of small mangrove islands known as cayes that constitute Turneffe Atoll. The single lagoon site, hereafter called Turneffe Lagoon, consists of a shallow patch reef (0.5–3.0 m deep) located in Long Bogue, just west of Calabash Caye. One of the two mangrove sites, called Calabash Channel, is located ~1.4 km east of the Turneffe Lagoon patch reef. Within Calabash Channel, we assessed corals growing on the prop roots of *R. mangle* in three locations where they are most abundant: (1) along the northern shore, (2) along the circumference of a small island, and (3) along the banks of a small creek that connects Calabash Channel to an expansive pond located within the interior of Calabash Caye. The second mangrove site we surveyed was at Crooked Creek, located on the western side of Turneffe Atoll, ~10.5 km west of the Turneffe Lagoon patch reef. Here, we monitored corals growing on *R. mangle* roots along an approximately 150-m stretch at the eastern edge of the creek, where it enters the central lagoon of Turneffe Atoll (Fig. 1B).

Environmental monitoring

From November 2017 to November 2018, five Onset HOBO Pendant data loggers (Onset Corporation, Bourne, MA) were deployed to record both temperature (°C) and light intensity (lux) every three hours. Three loggers were placed in Calabash Channel, dispersed between coral colonies that were surveyed. The loggers were affixed to bare mangrove roots (unshaded by epibionts), using nylon cable ties at approximately 40-cm depth, where mangrove corals are commonly found. Two loggers were placed in the Turneffe Lagoon patch reef site. For the light measurements, we utilized only the first seven days of recorded data because the instruments' sensitivity to light declined rapidly as a result of fouling by marine organisms. Data collected between 2000 hours and 0500 hours were removed (all values were 0 lux during this time window). Lux was converted to photosynthetic

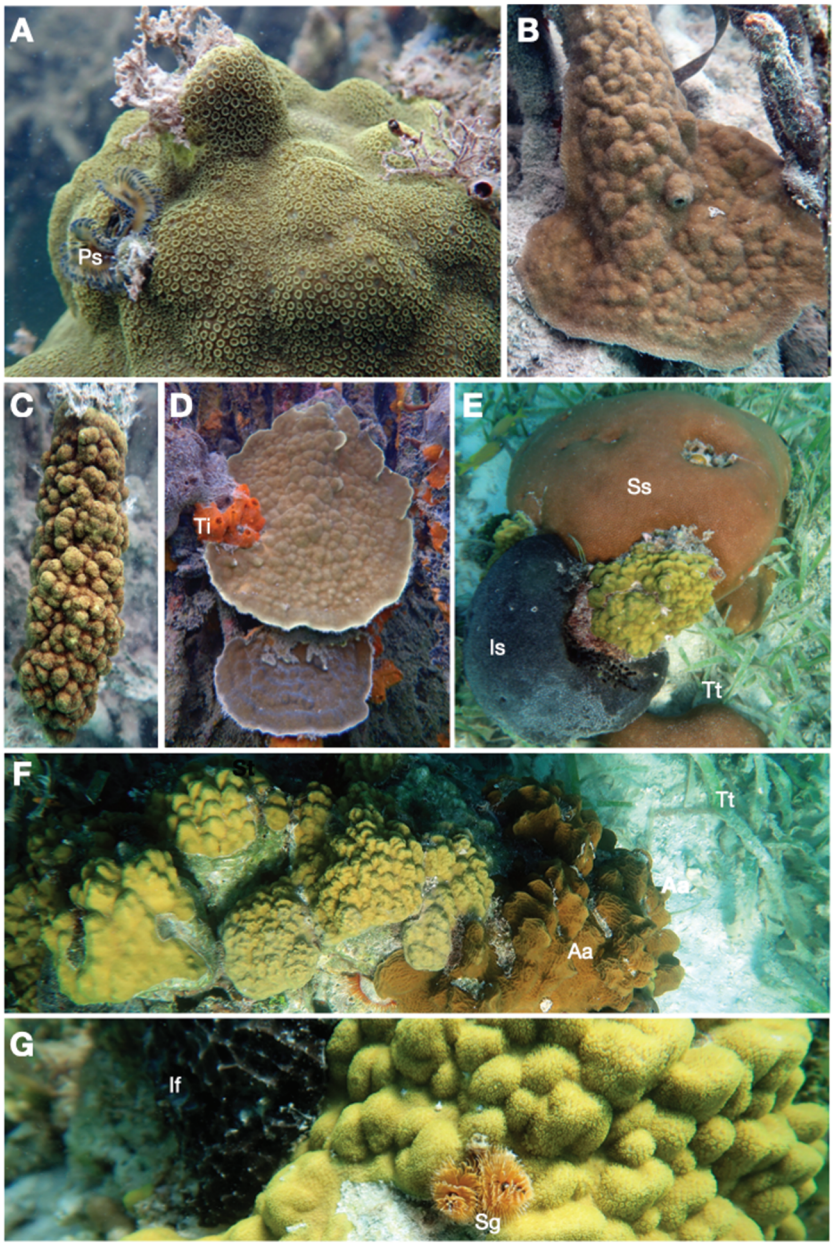

Figure 2. Representative photos of *Porites astreoides* from mangrove and lagoon habitats. (A) Coral growing on a mangrove root in Calabash Channel. (B–D) Corals growing on mangrove roots in Crooked Creek. (E–G) Corals living in lagoon at Long Bogue. Co-occurring organisms visible in this photograph include *Agaricia agaricites* (Aa), *Ircinia felix* (If), *Ircinia strobalina* (Is), *Pomatostegus stellatus* (Ps), *Spirobranchus giganteus* (Sg), *Siderastrea siderea* (Ss), *Tedania ignis* (Ti), and *Thalassia testudinum* (Tt).

photo flux density (PPFD: μmol m^{-2} s^{-1}) with a standard sunlight conversion factor of 0.0185. We recorded the depth of each colony at each site in 2018. In the lagoon, colony depth was measured with a Laylin Speedtech SM-5 portable sounder and depth meter (Laylin Associates, Unionville, VA). In the mangroves, colony depth was measured from the water's surface to the highest point of the colony by using a measuring tape.

Phenotypic characteristics

For each coral growing in the lagoon, height was measured as the vertical distance from the tallest part of the colony to its attachment with the substrate. Length and width were measured in a plane parallel to the substratum, with length representing the greatest linear dimension parallel to the substrate and with width measured at a point rotated 90° from where the

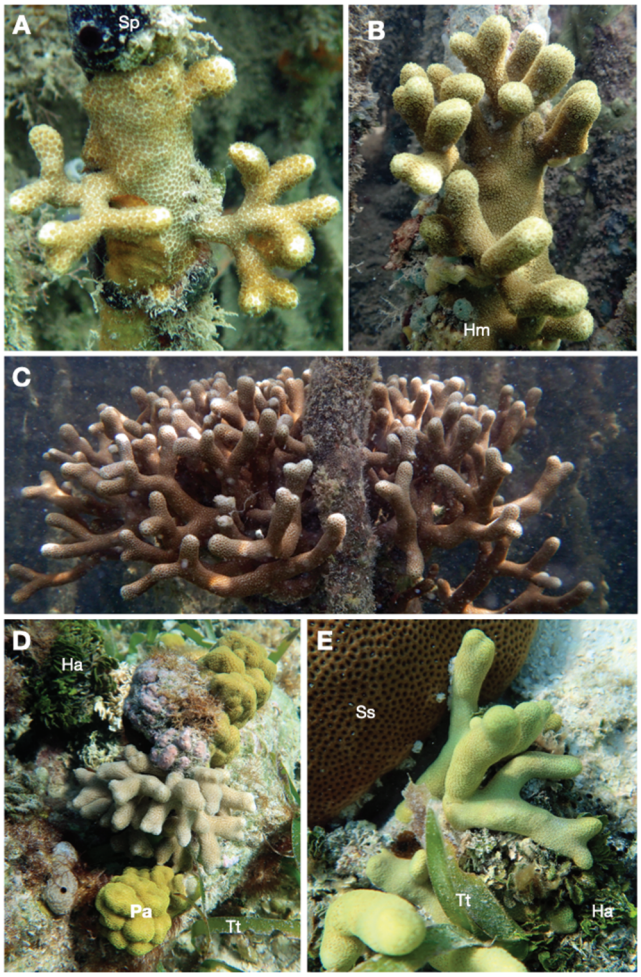

Figure 3. Representative photos of *Porites divaricata* from mangrove and lagoon habitats. (A–C) Corals growing on mangrove prop roots in Calabash Channel. (D, E) Corals growing in patch reef habitat in Long Bogue. Co-occurring organisms visible in these photos include *Halimeda sp.* (Ha), *Haliclona manglaris* (Hm), *Porites astreoides* (Pa), *Spongia pertusa* (Sp), *Siderastrea siderea* (Ss), and *Thalassia testudinum* (Tt).

length was taken. For corals growing on mangrove roots, linear dimensions were measured as previously described (Bengtsson *et al.*, 2019; Scavo Lord *et al.*, 2020). Height was measured as the perpendicular distance from the root to the most distant extent of the colony. Length was measured as the linear extent of the colony along the root, and width was measured at 90° to both height and length. From these linear dimensions, we calculated ecological volume as πHr^2, where H is equal to colony height and r is equal to (colony width + colony length)/4 (Shaish *et al.*, 2006).

Corals were photographed *in situ* against a laminated DKK color standard (DGK Color Tools) that included a six-step gray scale featuring true white, as well as 12% and 18% gray. Using the method presented by Winters *et al.* (2009), these photographs were used to estimate the chlorophyll density of each coral colony. Briefly, all photographs were standardized using the gray scale and the MATLAB (MathWorks, Natick, MA) macro CalibrateImageA. Then, the MATLAB macro AnalyzeIntensity was used to calculate mean red channel intensity for 20 swatches of 25 × 25 pixels for each coral. Higher red channel intensity values indicate fewer algal photosynthetic pigments (Winters *et al.*, 2009).

Branch diameter and branch tip number were recorded in the field while snorkeling. Branch diameter was measured using calipers at a point 2.5 cm below the branch tip for 3 branches selected haphazardly across the diameter of each colony, and the average value was calculated. For branch tip number, only visibly healthy branches at least ~1 cm in length were counted. Counts were performed a minimum of two times for each coral colony by the same surveyor, and the count was repeated if there was a discrepancy. Branch density (branch tips cm^{-3}) was calculated by dividing branch tip number by ecological volume.

The surface rugosity of *Porites astreoides* was determined using the bar and chain method (Risk, 1972) at each colony's widest point. Based on *in situ* observations corroborated by photographs, the form of each colony was characterized as mounding, plating, or a combination of mounding and plating; and the proportion of each form was compared between sites.

For both species, a flexible stencil of known area was placed flush against each coral's surface to obtain three macrophotographs of the corallites circumscribed by the stencil. The stencil was used to standardize the area in which the number of corallites was counted. In *Porites divaricata*, the 3 photographs were taken at a point 1.0 cm below the branch tip on 3 random branches; in *P. astreoides*, the photographs were taken at 3 random locations on the colony. From the photographs, corallite density and corallite area were determined. Corallite density was measured by counting all corallites whose central point was located within the circular frame and dividing by the area of the frame. The multipoint tracking tool of ImageJ (ver. 1.5a; https://imagej.nih.gov/ij/) was used to count the corallites present in the frame (Abramoff *et al.*, 2004). For each coral, the average corallite density was determined from the three photos taken. Corallite area was determined by manually tracing corallites in the photographs and calculating the area of the irregular shape, using ImageJ. Only corallites located entirely within the circular frame were included in the analysis. For each coral, the average corallite area was determined for the three photos taken. Corallite spacing was determined from photographs, using ImageJ, by measuring the distances between all pairs of adjacent corallite centers located within the circular frame. For each coral, the average distance between corallites was determined for the three photos taken.

For all phenotypic variables—ecological volume, color intensity, branch diameter, branch density, branch tip number, surface rugosity, corallite density, corallite area, and corallite spacing—we compared mean values for mangrove *versus*

Table 1

Average branch diameter in Porites divaricata*,* Porites furcata*, and* Porites porites

Sample	*n*	Branches measured	Average branch diameter (cm)	Standard error
Calabash Channel	58	174 (3 per colony)	0.78	0.02
Crooked Creek	15	45 (3 per colony)	0.72	0.03
All Mangrove	73	219 (3 per colony)	0.78	0.02
Long Bogue	31	93 (3 per colony)	0.76	0.02
Dimond *et al.* group 1	5	5 (widest branch)	0.88	1.3
Dimond *et al.* group 2	10	10 (widest branch)	1.76	2.1
Dimond *et al.* group 3	12	12 (widest branch)	1.08	1.6

Samples for groups 1–3 are from Dimond et al. (2017).

lagoon samples from each species. Data from Calabash Channel and Crooked Creek were combined to generate an average value for mangrove specimens because there were no significant differences between the two mangrove sites for any of the phenotypic variables (Figs. A1–A7). If the raw data or logarithmically transformed data met the assumption of normality according to a Shapiro-Wilk test, an independent-sample *t* test was conducted to compare means. Prior to testing, an *F* test was performed to determine whether there were significant differences in the variances between the two sites. Samples exhibiting unequal variances were compared using a Welch's *t* test, and those exhibiting equal variances were compared using a Student's *t* test. If the data violated the assumption of normality, even following ln transformation, a Mann-Whitney-Wilcoxon test (non-parametric) was conducted. In these cases, homogeneity of variances was determined with a Brown-Forsythe test. Differences between means were regarded as significant for $P < 0.05$. Each test was conducted both with and without outliers (if present). Outliers were removed using the boxplot$out command in R (R Core Team, 2018), which identifies the values lying further than 1.5 times the interquartile range from the upper and lower quartiles. In general, the removal of outliers had a negligible impact. In two instances (branch density and corallite spacing), removal of outliers resulted in a comparison between mangrove and lagoon exhibiting statistical significance ($P < 0.05$) where it was not otherwise significant. Therefore, all analyses and resulting figures with outliers removed are included in Figures A2–A8, while all main text analyses and figures include outliers.

Results

Over the course of 2 sampling periods (November 2018 and November 2019), we obtained data from 249 distinct coral individuals: 155 specimens of *Porites divaricata* and 94 specimens of *Porites astreoides* (Table 2). The 146 specimens assessed in 2018 were used for the analyses of ecological volume, branch number, branch density, branch diameter, and surface rugosity. The 103 specimens assessed in 2019 were used for the analyses of corallite density, corallite area, corallite spacing, and colony color.

Environmental variation across habitats

The mangrove and lagoon habitats were significantly different with respect to temperature, light, and the average depth at which corals were located (Figs. 4, A1). From November 2017 to December 2018, the average temperature in the mangroves of Calabash Channel was significantly warmer than in the lagoon at Long Bogue (mean ± SD, 28.77 °C ± 1.84 °C *vs.* 28.62 °C ± 1.79 °C, respectively, $P = 0.038$; Fig. 4A). Furthermore, the average daily temperature variance at Calabash Channel was significantly greater than at Long Bogue

Table 2

Specimens analyzed by habitat, site, and species

Date	Habitat	Site	No. *Porites divaricata*	Phenotypic trait measured	No. *Porites astreoides*	Phenotypic trait measured
January 2018	Mangrove	Calabash Channel	58	Ecological volume, branch tip number, branch density, branch diameter	0	Ecological volume, rugosity
		Crooked Creek	15		22	
	Lagoon	Long Bogue	31		20	
January 2019	Mangrove	Calabash Channel	22	Colony color, corallite density, corallite area, corallite spacing	1	Colony color, corallite density, corallite area, corallite spacing
		Crooked Creek	6		22	
	Lagoon	Long Bogue	23		29	
Total			155		94	

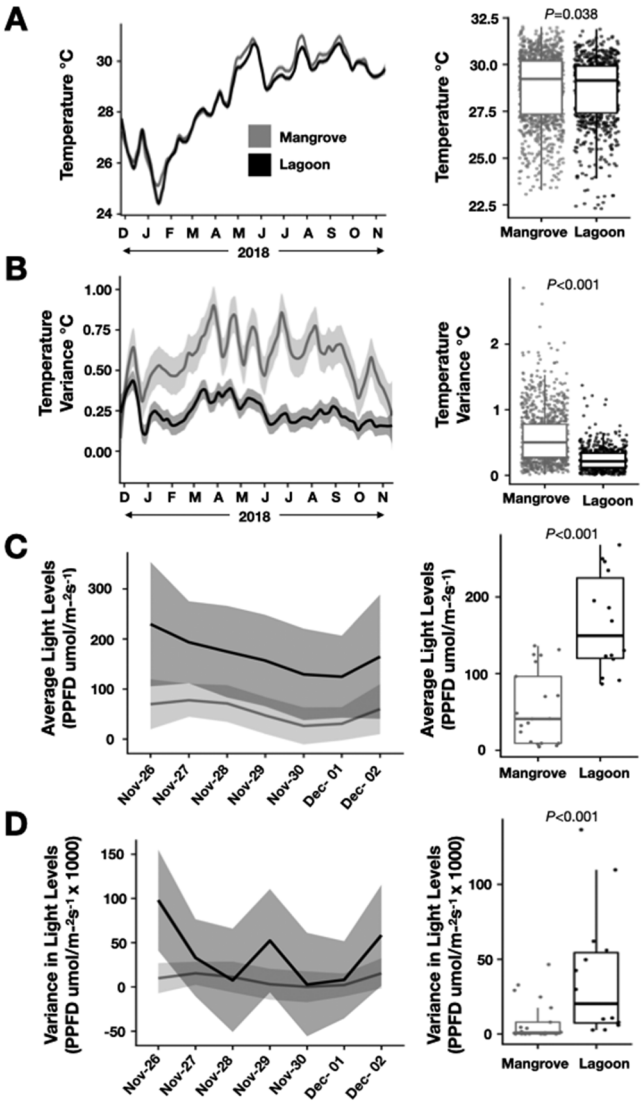

Figure 4. Environmental differences between lagoon and mangrove sites. (A) Mean daily temperature tracked over a 12-month period (left) and averaged over the entire period (right). (B) Daily temperature variance tracked over a 12-month period (left) and averaged over the entire period (right). (C) Mean daily light levels tracked over a 7-day period (left) and averaged over the entire period (right). (D) Daily light variance tracked over a 7-day period (left) and averaged over the entire period (right). In the panels on the left, the shaded areas around the lines indicate standard error. In the panels on the right, each point on the graph represents a single light measurement. The line dividing the box into two sections represents the mean, the top and bottom lines of the box denote the first and third quartile, and the whiskers represent the largest and smallest value that lie within 1.5 times the interquartile range. PPFD, photosynthetic photo flux density.

(0.58 °C ± 0.39 °C *vs.* 0.24 °C ± 0.17 °C, respectively, $P < 0.001$; Fig. 4B). The average light levels were significantly greater in the lagoon than in the mangroves (165.39 ± 64.45 μmol m^{-2} s^{-1} *vs.* 54.50 ± 47.96 μmol m^{-2} s^{-1}, respectively, $P < 0.001$; Fig. 4C), as was the daily variation in light levels (38,085.62 ± 41,957.42 *vs.* 8180.02 ± 13,606.61, respectively, $P < 0.001$; Fig. 4D). For both species, mean colony depth was significantly greater in the lagoon than in the mangroves (Fig. A1).

Phenotypic characteristics

For both coral species, the mean ecological volume was greater for the lagoon samples than the mangrove samples (Fig. 5), although the difference was statistically significant only for *P. divaricata* ($P < 0.001$; Fig. 5A). In *P. divaricata*, the variances between mangrove and lagoon samples were significantly different ($P < 0.001$). The mangrove samples for *P. divaricata* exhibited by far the greatest size range, from 3.62 to 18, 117.25 cm^3 (Fig. 5A). *Porites astreoides* from the lagoon exhibited the next greatest size range, from 271.89 to 16,679.96 cm^3 (Fig. 5B); however, the variances between mangrove and lagoon samples were not significantly different ($P = 0.26$).

For both coral species, the mangrove colonies exhibited significantly greater intensity in the red color channel than lagoon colonies (Fig. 6). The differences between mangrove and lagoon colonies were statistically significant at $P < 0.001$ for both *P. divaricata* (Fig. 6A) and *P. astreoides* (Fig. 6B). In *P. divaricata*, the range of color intensity values was greater in the mangroves than in the lagoon (54.5–173.6 *vs.* 90.3–190.5). In *P. astreoides*, the range of color intensity values was greater in the lagoon (93.6–179.5 *vs.* 46.1–113.9). However, in both species the variances between mangrove and lagoon samples were not significantly different ($P = 0.82$ and $P = 0.73$ for *P. divaricata* and *P. astreoides*, respectively). For these analyses, the intensity for the red channel was used because it is known to have the highest correlation with chlorophyll density (Winters *et al.*, 2009); however, mangrove corals also exhibited significantly greater color intensity in both the green and blue channels (Fig. A8).

Branch tip number was the only branch metric that exhibited a clear difference between mangrove and lagoon *P. divaricata* (Fig. 7A). On average, lagoon colonies had about twice as many branches as mangrove colonies (44.8 *vs.* 22.2 branches; Fig. 7A). These differences were highly significant ($P < 0.001$). Mangrove colonies exhibited a greater range of branch numbers (1–157) than lagoon colonies (10–83), but the variances between mangrove and lagoon samples were not significantly different ($P = 0.9$).

Branch density did not differ between mangrove and lagoon samples unless outliers were removed (Figs. 7B, A6B). With outliers included, the mean branch density of lagoon corals was less than that of mangrove corals (0.03 ± 0.01 *vs.* 0.04 ± 0.07 branches cm^{-3}, respectively, $P = 0.10$; Fig. 7B). With outliers excluded, the mean branch density of lagoon corals exceeded that of mangrove corals (0.03 ± 0.01 *vs.* 0.02 ± 0.02 branches cm^{-3}, respectively, $P = 0.008$; Fig. A6B). Mangrove colonies showed a higher range in branch density values than lagoon colonies (0.004–0.55 *vs.* 0.01–0.06 branches cm^{-3}, respectively), but the variances

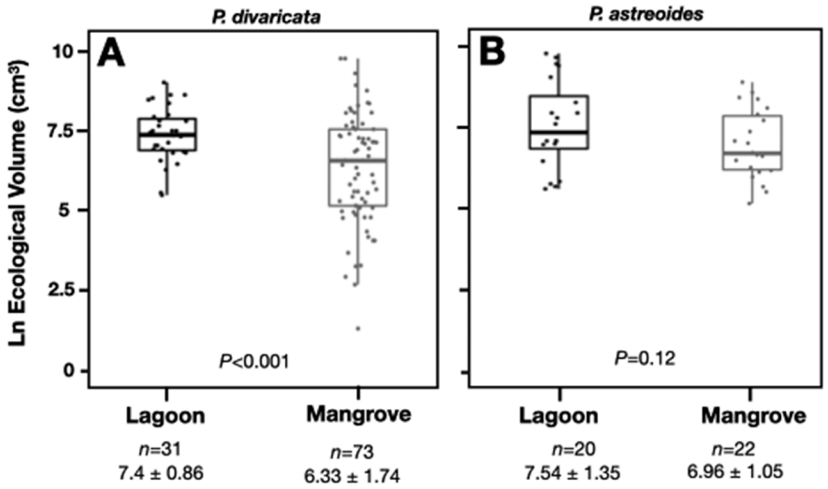

Figure 5. Ecological volume of *Porites divaricata* (A) and *Porites astreoides* (B) in lagoon and mangrove environments. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest value that lie within 1.5 times the interquartile range. Statistically significant differences in ecological volume between sites were determined with a Welch two-sample *t* test for *P. divaricata* and a Student's two-sample *t* test for *P. astreoides*.

between mangrove and lagoon samples were not significantly different ($P = 0.17$).

There was no significant difference in average branch diameter between mangrove and lagoon habitats (Fig. 7C). However, we again observed a greater range of values in the mangroves (0.35–1.2 cm) than in the lagoon habitat (0.6–0.9 cm), and the variances between mangrove and lagoon samples were significantly different ($P = 0.001$).

Porites astreoides exhibited significantly higher mean rugosity in the lagoon than in the mangrove ($P = 0.04$; Fig. 8A). The range of rugosity was greater between mangrove corals (1.07–2.46) than between lagoon corals (1.04–2.09), but the variances between mangrove and lagoon samples were not significantly different ($P = 0.21$). The lagoon site exhibited much greater consistency in form, with 100% of colonies surveyed exhibiting a mounding phenotype

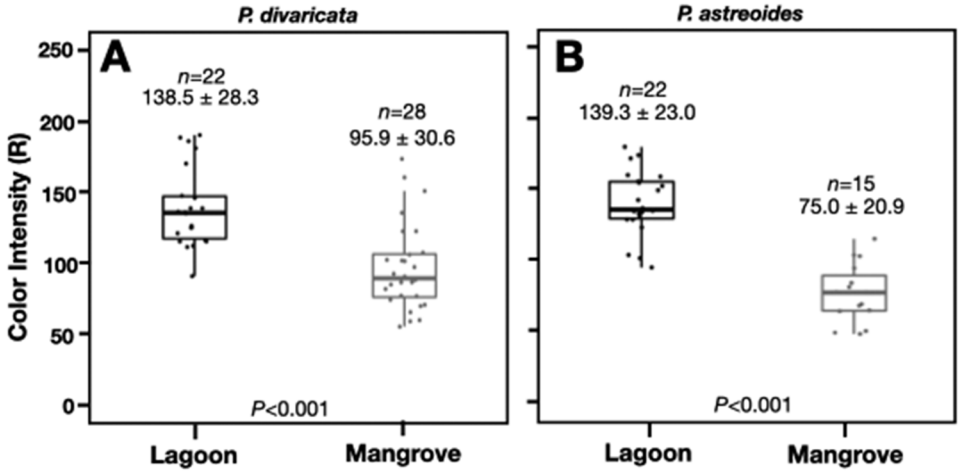

Figure 6. Colony color of *Porites divaricata* (A) and *Porites astreoides* (B) in lagoon and mangrove environments. Red, R, channel intensity is a proxy for chlorophyll pigment density, with higher-intensity values corresponding to lower chlorophyll densities. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest value that lie within 1.5 times the interquartile range. Statistically significant differences in colony color between sites were determined with a Mann-Whitney-Wilcoxon test in *P. divaricata* and a Student's two-sample *t* test in *P. astreoides*. An independent *t* test was also performed on ln-transformed *P. divaricata* values because transformation resulted in normalized data ($P < 0.001$); however, in order to display the values on the same scale as *P. astreoides*, we conducted the analysis on the non-transformed data.

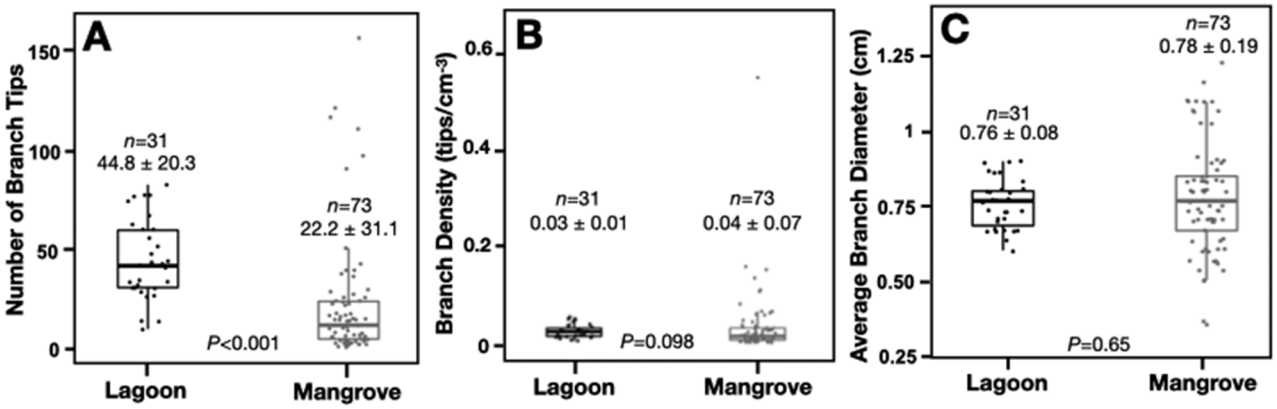

Figure 7. Branch tip number (A), branch density (B), and average branch diameter (C) in *Porites divaricata*. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest value that lie within 1.5 times the interquartile range. Statistically significant differences in all three branch metrics between sites were determined with a Mann-Whitney-Wilcoxon test.

(Fig. 8B). The majority of mangrove corals (59%) exhibited a plating morphology (*e.g.*, Fig. 3D), while only 27% exhibited a mounding form (*e.g.*, Fig. 3C), and 14% exhibited a combination of plating and mounding (*e.g.*, Fig. 3B).

In both species, average corallite density was significantly greater in the mangrove samples than the lagoon samples ($P < 0.001$; Fig. 9A, D). For *P. divaricata*, mangrove colonies exhibited a greater range of corallite density values (57.7–130.7 corallites cm^{-2}) than lagoon colonies (46.6–109.4 corallites cm^{-2}; Fig. 9A). The same was true for *P. astreoides*, with ranges of 51.4–118.2 and 46.0–75.8 corallites cm^{-2} in the mangrove and lagoon samples, respectively (Fig. 9D). In both species, the variances between mangrove and lagoon samples were significantly different ($P = 0.04$ and $P < 0.001$ for *P. divaricata* and *P. astreoides*, respectively).

Average corallite area was slightly higher in lagoon *versus* mangrove samples of both corals (Fig. 9B, E), although only the difference in *P. divaricata* was statistically significant ($P = 0.02$). The range of corallite areas for the lagoon samples of *P. divaricata* (0.52–1.42 mm^2) was slightly higher than the corresponding values for the mangrove samples (0.58–1.38 mm^2), but the variances were not significantly different

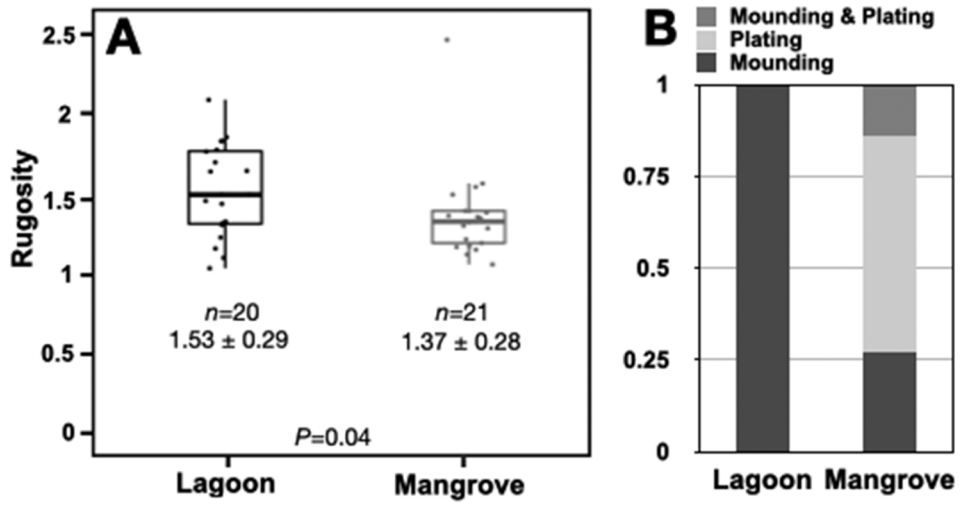

Figure 8. Rugosity and form in *Porites astreoides.* (A) Mean rugosity. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest value that lie within 1.5 times the interquartile range. (B) Relative abundance of three *P. astreoides* colony forms: plating, encrusting, or a combination of both. Statistically significant differences in rugosity between sites were determined with a Mann-Whitney-Wilcoxon test.

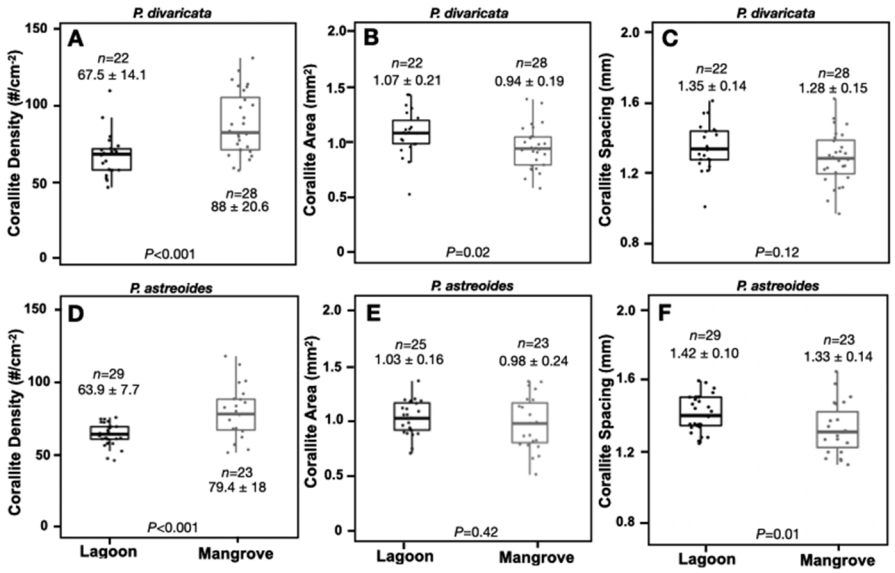

Figure 9. Corallite density, area, and spacing in *Porites divaricata* and *Porites astreoides* from lagoon and mangrove environments. Mean corallite density, area, and spacing in *P. divaricata* (A, B, C, respectively) and *P. astreoides* (D, E, F, respectively). Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest value that lie within 1.5 times the interquartile range. Statistically significant differences in corallite density between sites for *P. divaricata* were determined with a Mann-Whitney-Wilcoxon test. Statistically significant differences in corallite density and area in *P. astreoides* were determined with a Welch two-sample *t* test, and corallite area and spacing in *P. divaricata* and corallite spacing in *P. astreoides* were determined with a Student's two-sample *t* test.

($P = 0.71$); the opposite trend was seen in *P. astreoides* (0.51–1.37 and 0.71–1.37 mm^2 for the mangroves and lagoon, respectively). The variances between mangrove and lagoon samples were significantly different in *P. astreoides* ($P = 0.04$).

Similar to average corallite area, average corallite spacing was also slightly higher in lagoon *versus* mangrove samples in both species (Fig. 9C, F). Only the difference in *P. astreoides* was statistically significant ($P = 0.01$); however, the difference in *P. divaricata* was significant when outliers were excluded ($P = 0.04$). The range of corallite spacing for the lagoon samples of *P. divaricata* (1.01–1.61 mm) was slightly higher than the corresponding values for the mangrove samples (0.97–1.62 mm), while the opposite trend was observed in *P. astreoides* (1.13–1.66 and 1.25–1.60 mm for the mangroves and lagoon, respectively); but in both species, the variances between mangrove and lagoon samples were not significantly different ($P = 0.64$ and $P = 0.08$ for *P. divaricata* and *P. astreoides*, respectively).

Discussion

Mangroves are increasingly being recognized as an important component of the ecological niche for many coral species (Yates *et al.*, 2014; Hernández Fernández, 2015; Rogers, 2017; Bengtsson *et al.*, 2019; Camp *et al.*, 2019; Kellogg *et al.*, 2020; Scavo Lord *et al.*, 2020). Here, we demonstrate significant differences in key environmental variables between the mangrove and adjacent coral-supporting habitats. We also document a number of statistically significant differences in the phenotype of coral colonies in mangrove and lagoon habitats, including differences in colony size, color, structural complexity, and corallite morphology. For each phenotypic trait, the direction of the difference between mangrove and lagoon corals was consistent in *Porites divaricata* and *Porites astreoides*; for example, both species exhibited lower ecological volume, lower color intensity, and greater corallite density in the mangroves compared to the lagoon.

With respect to size, lagoon corals exhibited a larger mean ecological volume than mangrove corals, although the difference was statistically significant only in *P. divaricata*. Differences in overall colony size could reflect size constraints on corals growing in the mangroves. In the mangrove habitats studied, all colonies were found growing directly on prop roots, which can be either grounded in the peat bank or aerially suspended. On grounded roots, lateral expansion of colonies is typically constrained by other roots and/or root epibionts, and vertical expansion is constrained by the water's surface and shallow peat bank. In contrast, aerial roots are not attached to the shallow peat bank, but extend outward from the bank and hang vertically into the water column. Colonies settling on these roots have more space to grow,

because they are not constrained by other roots and/or epibionts; the largest colonies we observed were often situated on such aerial roots. However, such large colonies are more directly exposed to the currents, putting the corals at greater risk of being dislodged during a storm. The colonies may also grow too heavy for the root to support. This could result in wholesale loss of the colony and possibly accelerated breakage of the root. This phenomenon has previously been observed during longitudinal monitoring of mangrove sponges (Bingham and Young, 2005) and mangrove corals (Scavo Lord *et al.*, 2020).

The lagoon might also support larger colonies as a result of greater energetic resources available *via* photosynthetic byproducts of Symbiodiniaceae, because light availability has been correlated with increased growth rates in a number of coral species, including *P. astreoides* (Huston, 1985). We suspect that variability in light levels could explain the greater range of colony sizes in mangrove *P. divaricata*, but our existing light data lack the spatial resolution necessary to test this hypothesis. In the current study, three light meters were deployed adjacent to corals in typical mangrove locations, where they were shaded by the canopy throughout much of the day. As a result, the measured light levels were relatively low and invariant. While these shaded locations are where we most often observed corals, we have observed that the largest colonies tend to be found on roots that extend out from beneath the canopy (on aerial roots), where they would be exposed to more light. We suspect that there are more corals on shaded roots because such roots are more abundant, not because they represent preferable habitat. However, one advantage of the shadier, less exposed (ground) roots is that they tend to be simultaneously less vulnerable to strong currents, which could cause the root to break or the coral to become dislodged from the root. In addition, coral colonies shaded by roots have been found to suffer less bleaching and mortality than unshaded colonies (Yates et al., 2014). Future studies could test the significance of fine-scale variation in light and flow by deploying a larger number of light and flow meters immediately adjacent to mangrove corals spanning a wide range of sizes.

For both species, colonies in the lagoon exhibited greater color intensity than colonies in the mangroves. Because higher intensity of the red channel is inversely correlated with chlorophyll density (Winters *et al.*, 2009), this suggests that mangrove colonies exhibit higher chlorophyll pigment density than conspecifics in the lagoon. Elevated chlorophyll concentration is a well-characterized adaptive response to maximize light harvesting by photosynthetic symbionts in corals inhabiting low-light environments (Abramovitch-Gottlib *et al.*, 2005; Stambler and Dubinsky, 2005). The same trend was documented in a comparison of mesophotic (45–50 m) *versus* shallow (20–25 m) colonies of *Montastrea cavernosa* (Linnaeus, 1767), where mesophotic colonies contained significantly more Symbiodiniaceae cells, chlorophyll *a* per Symbiodiniaceae cell, and chlorophyll *a* and c_2 per unit area (Polinski and Voss, 2018). Similarly, increasing chlorophyll concentrations were observed in branch fragments of *Stylophora pistillata* Esper, 1797 transplanted to lower light levels (from 95% to 0.8% photosynthetic active radiation, PAR_0) (Titlyanov *et al.*, 2001).

The observed differences in colony form between habitats might also be attributable to variation in light (Todd, 2008). In *P. astreoides*, the hemispherical mounding phenotype was found exclusively in the lagoon, while the plating, more flattened form was common in the mangroves. Variation in growth forms in differing light regimes is thought to be an adaptive response to maximize light capture in low-light environments or enable self-shading in extremely high-light environments (Klaus *et al.*, 2007). For example, colonies of *Porites rus* (Forskål, 1775) (formerly *Synaraea rus* Forskål, 1775) exposed to high light levels exhibited hemispherical forms with short branches, while colonies exposed to the lowest light levels exhibited explanate or plating forms (Jaubert, 1977). Similarly, the boulder star coral, *Orbicella annularis* (Ellis & Solander, 1786), maximizes light capture in low light by growing in a flattened growth form (Dustan, 1975).

Differences in corallite morphology were also consistent across habitats. Mean corallite density was higher in mangrove *versus* lagoon colonies for both species. Simultaneously, mean corallite area was also smaller in mangrove *versus* lagoon colonies, but this result was significant only in *P. divaricata.* Light availability has been linked to various aspects of corallite morphology. In particular, lower light is associated with decreasing corallite size (Beltran-Torres and Carricart-Gavinet, 1993), as in *M. cavernosa*, where mesophotic colonies were found to have smaller corallites than shallow conspecifics (Studivan *et al.*, 2019). Light availability can also influence the spacing between corallites, and corals exposed to lower light have been shown to exhibit a greater degree of spacing between corallites (Studivan *et al.*, 2019). However, at odds with these findings from other corals exposed to lower light levels (Studivan *et al.*, 2019), individuals of *P. divaricata* and *P. astreoides* in the mangroves exhibited a lower degree of corallite spacing than those in the lagoon. Nevertheless, mangrove representatives of *P. divaricata* did exhibit significantly smaller corallite area, and smaller corallites or smaller polyps generally are suspected to maximize surface area for food capture (Sebens, 1997). Therefore, smaller corallite size, and a higher density of corallites per unit area, might suggest a greater reliance on heterotrophy in lower or more variable light environments, such as the mangroves. This reliance on heterotrophy may be particularly advantageous in mangrove habitats, which could compensate for lower and more variable light availability. In the temperate coral *Cladocora caespitosa* (Linnaeus, 1767), corals maintained in a low-light environment used nutrients from heterotrophy to supplement calcification, and corals under high light converted carbon from feeding to tissue biomass (Hoogenboom *et al.*, 2008). Similar

heterotrophic plasticity was observed in a laboratory study of *Goniastrea retiformis* (Lamarck, 1816), which increased its feeding rate to fully compensate for reduced phototrophy when light levels were attenuated by suspended particulate matter; interestingly, under the same conditions, *Porites cylindrica* Dana, 1846 increased heterotrophy only slightly and lost energy reserves as a result (Anthony and Fabricius, 2000). Consumption of dissolved nutrients may also be an important contributor to heterotrophy in the nutrient-rich mangroves. For example, mangroves are particularly rich sources of dissolved organic carbon (Dittmar *et al.*, 2006). Uptake of dissolved organic carbon has been shown to occur in some corals, including both *P. astreiodes* and *P. divaricata*, where it can mitigate the loss of autotrophic nutrients during annual bleaching (Levas *et al.*, 2016). Plasticity in trophic strategies could be an important survival strategy in corals that are able to exploit mangrove habitats; but the relative reliance on heterotrophy and autotrophy could impact different biological processes differently, as in the facultatively symbiotic *Astrangia poculata* (Ellis & Solander, 1786), where wound healing and total tissue cover were impacted differently by autotrophy and heterotrophy (Burmester *et al.*, 2018).

Phenotypic variability has been widely documented in corals spanning a range of environmental gradients. The consistent phenotypic differences across habitat types in the two species described here could be driven by constraints imposed by the habitat, phenotypically plastic responses to environmental variation, genetic differences due to the selection of locally advantageous phenotypes, or any combination of the above. Although measured or observable habitat constraints (*i.e.*, prop root positioning) are touched on here, other environmental constraints not measured (*i.e.*, pH) could also contribute to phenotypic differences between sites. For instance, Camp *et al.* (2016) documented suppressed rates of calcification and photosynthesis in corals occupying unshaded locations adjacent to mangroves compared to corals inhabiting seagrass, back-reef, and outer-reef habitats. These responses were attributed to lower mean pH at the two mangrove sites located in the Indian and Pacific Ocean regions (Camp *et al.*, 2016). Going forward, pH may be a critical environmental parameter to measure, given its effect on coral phenotype, and may be site specific. For example, coral-dominated mangroves in the U.S. Virgin Islands were characterized with higher pH than nearby reef habitats (Yates *et al.*, 2014). While more research is needed to determine the degree to which phenotypic plasticity is driving the observed differences (*i.e.*, reciprocal transplants of coral genets between habitats), we suspect that it plays a prominent role in the variation described here. First, all phenotypic differences observed between sites are consistent with documented trends in other coral species in low-light *versus* high-light environments. Importantly, there are many other environmental parameters that are known to drive phenotypic variation, including flow (Kaandorp *et al.*, 1996; Bruno and Edmunds, 1998), sedimentation (Todd *et al.*, 2001), and nutrient levels (Bongiorni *et al.*, 2003a, b). These other factors are also likely to contribute to variation in phenotypes between mangrove and reef corals of the same species, because mangroves are generally more stagnant, turbid, and nutrient rich compared to reefs (Nagelkerken *et al.*, 2008; Granek *et al.*, 2009). Additionally, with nearly every phenotypic trait, mangrove corals exhibited greater variability. This may reflect greater micro-environmental variation in the mangroves than the lagoon. For example, different prop roots can be exposed to very different light levels or flow patterns, depending on their distance from the peat bank, canopy, or other roots (Farnsworth and Ellison, 1996).

As described in the Introduction, there is disagreement in the literature over the species status of Caribbean branching *Porites*. Consistent with current taxonomy, which is supported by multiple studies employing both morphological and molecular criteria (Weil, 1992; Jameson, 1997; Forsman *et al.*, 2008; Jameson and Cairns, 2012; Dimond *et al.*, 2017), the current study treats *P. divaricata* as a distinct species, distinguishable in the field from *Porites furcata* and *Porites porites* on the basis of differences in branch diameter and habitat preference. Importantly, in the current study, we selected the colonies with the smallest branch diameters in both mangrove and lagoon habitats, and average branch diameter did not differ between habitats (Table 1; Fig. 7C). However, some studies have been unable to discriminate these species by using morphological or molecular criteria (Brakel, 1977; Prada *et al.*, 2014). If, as these studies suggest, these Caribbean branching *Porites* species constitute a single morphologically variable species, the interpretation of our findings would not be qualitatively altered. The differences we observed in the phenotype of mangrove and lagoon specimens of *P. divaricata* would still represent intraspecific differences that are associated with habitat, potentially attributable to environmental plasticity, local adaptation, or a combination thereof. A third possibility, not explicitly mentioned in the literature, is that *P. divaricata* is a distinct species but not readily distinguishable from *P. furcata* and/or *P. porites* in the field. Under this scenario, it is possible that we were comparing individuals from different species. If there were a systematic bias in the distribution of cryptic species between mangrove and lagoon, any habitat-associated differences we observed might have been conflated with species-specific differences.

To our knowledge, this is the first study to directly compare the phenotype of corals inhabiting mangrove prop root and shallow lagoonal patch reef habitats. Given increasing interest in the role of non-reef habitats for supporting coral resilience (Yates *et al.*, 2014; Hernández Fernández, 2015; Rogers, 2017; Bengtsson *et al.*, 2019; Camp *et al.*, 2019; Kellogg *et al.*, 2020; Scavo Lord *et al.*, 2020), it is important to understand whether and how coral phenotypes can change to accommodate the conditions found in what have historically been regarded as suboptimal habitats for corals, such as mangroves. The data presented here document intraspecific phenotypic differences in

two species between one lagoon site and two mangrove sites on Turneffe Atoll. To understand the generality of the habitat-phenotype associations we observed, it will be critical to replicate this study across additional mangrove and lagoon and/or reef sites and across more coral species. Going forward, it will also be important to differentiate genetic from environmental factors in the phenotypic diversity documented here. Toward this end, ongoing research is investigating (1) the effects of transplanting corals within and between mangrove and lagoon habitats and (2) the genetic differences between mangrove and lagoonal populations of *Porites* collected from the sites used in this study.

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Appendix

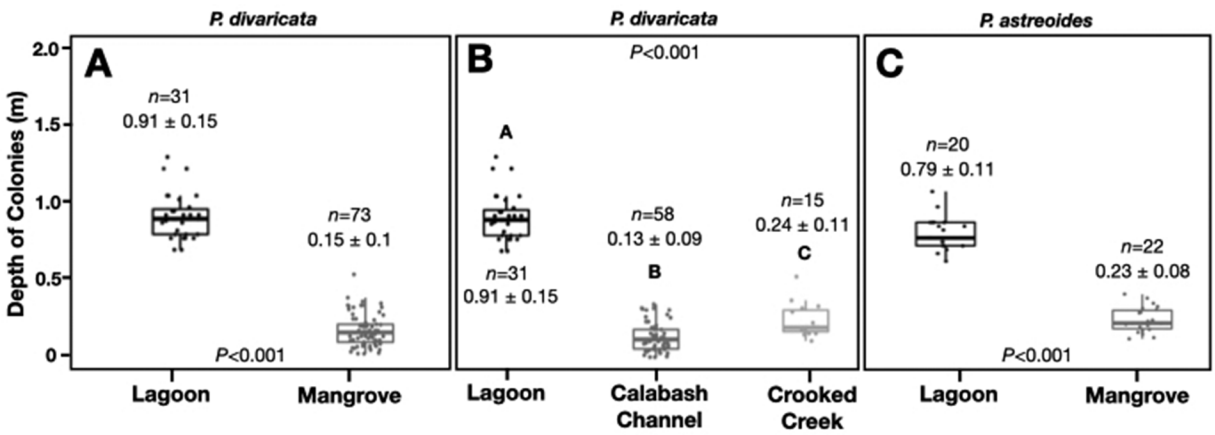

Figure A1. Colony depth between sites. Mean colony depth in *Porites divaricata*, when mangrove sites were pooled (A) and separated (B), and mean colony depth in *Porites astreoides* (C). The uppercase letters in (B) indicate that each of the three means is significantly different from the other two. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences in colony depth between the two sites were determined with a Mann-Whitney-Wilcoxon test in *P. divaricata* and a Student's two-sample *t* test in *P. astreoides*. When mangrove sites were separated, statistically significant differences were determined with an ANOVA and a Tukey *post hoc* test.

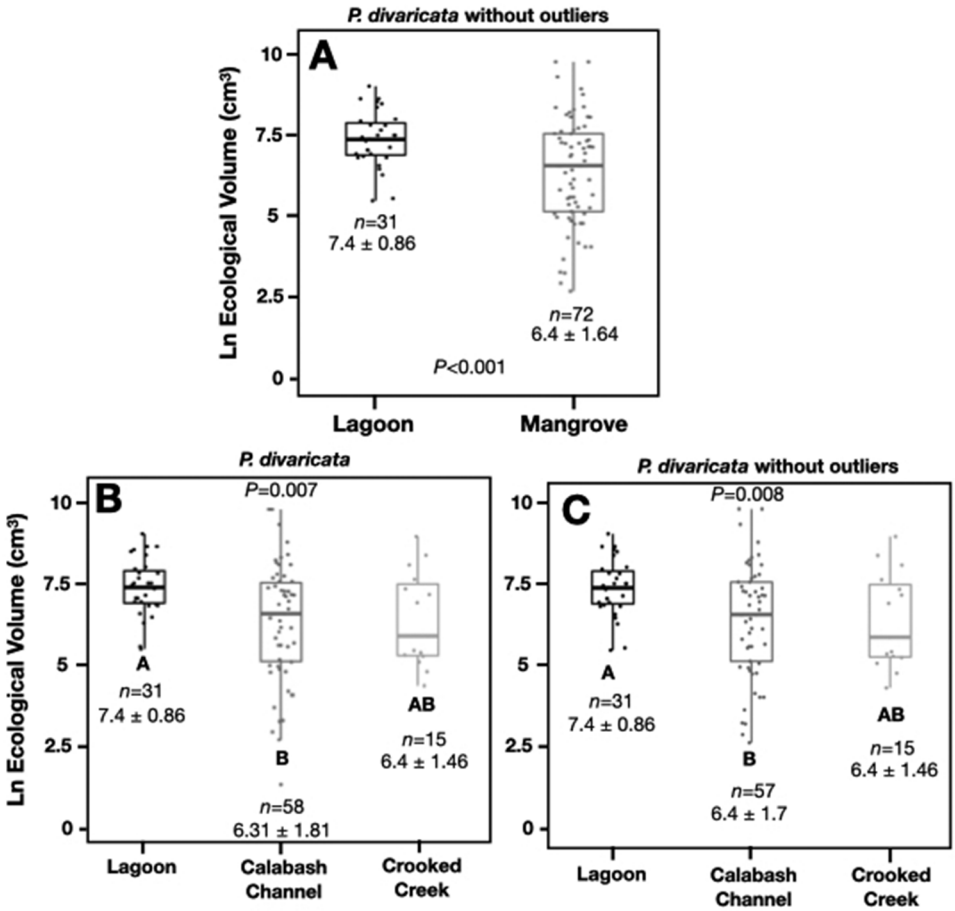

Figure A2. Boxplots depicting ecological volume of *Porites divaricata* in lagoon and mangrove environments when outliers were excluded (A) and when mangrove sites were separated, including (B) and excluding (C) outliers. The uppercase letters in (B) and (C) indicate that each of the three means is significantly different from the other two. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences between the two sites were determined with a Welch two-sample *t* test. When mangrove sites were separated, statistically significant differences were determined with an ANOVA and a Tukey *post hoc* test.

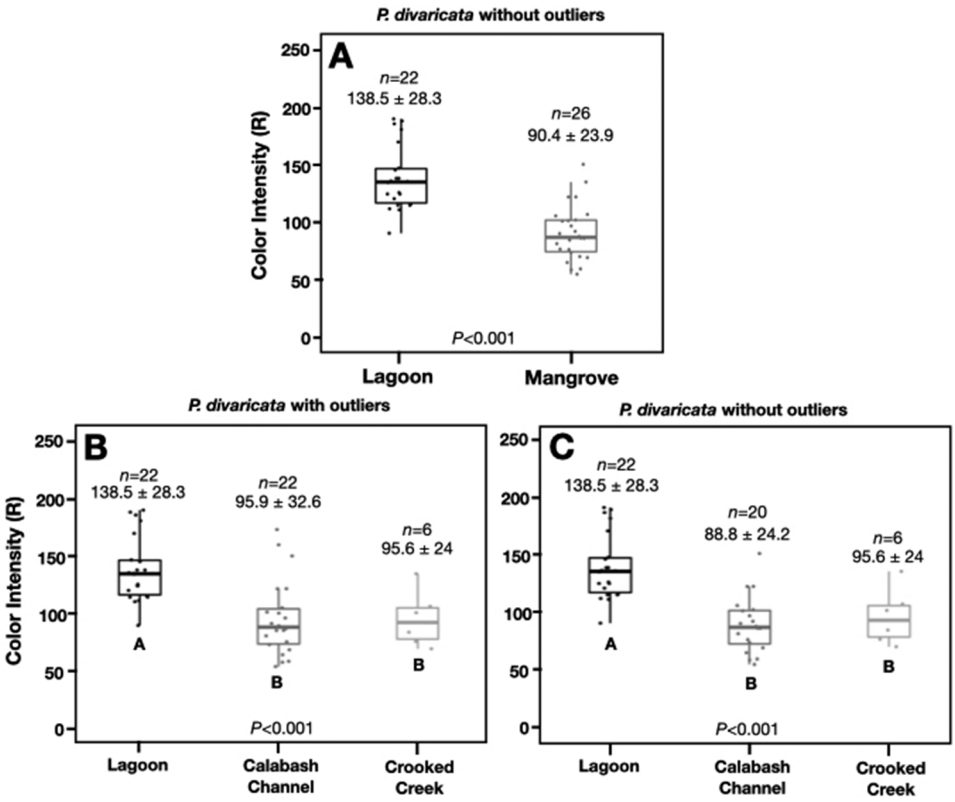

Figure A3. Boxplots depicting color intensity in the red, R, channel of *Porites divaricata* in lagoon and mangrove environments when outliers were excluded (A) and when mangrove sites were separated, including (B) and excluding (C) outliers. The uppercase letters in (B) and (C) indicate that each of the three means is significantly different from the other two. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences between the two sites were determined with a Mann-Whitney Wilcoxon test. When mangrove sites were separated, statistically significant differences were determined with Kruskal-Wallis and Dunn's tests.

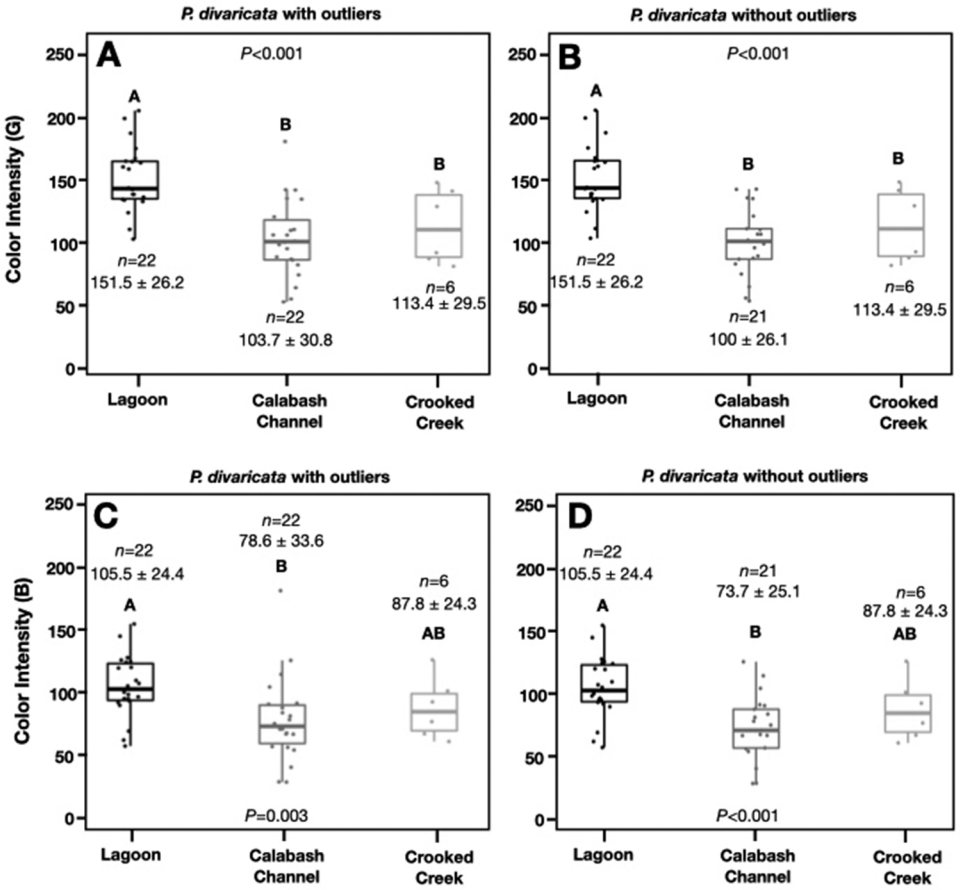

Figure A4. Boxplots depicting color intensity in the green, G, and blue, B, channels of *Porites divaricata* when mangrove sites were separated, including (A, C) and excluding (B, D) outliers. The uppercase letters in (A)–(D) indicate that each of the three means is significantly different from the other two. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences were determined with an ANOVA and a Tukey *post hoc* test in the green channel. Statistically significant differences in color intensity in the blue channel were determined with Kruskal-Wallis and Dunn's tests when outliers were included and with an ANOVA and a Tukey *post hoc* test when outliers were excluded.

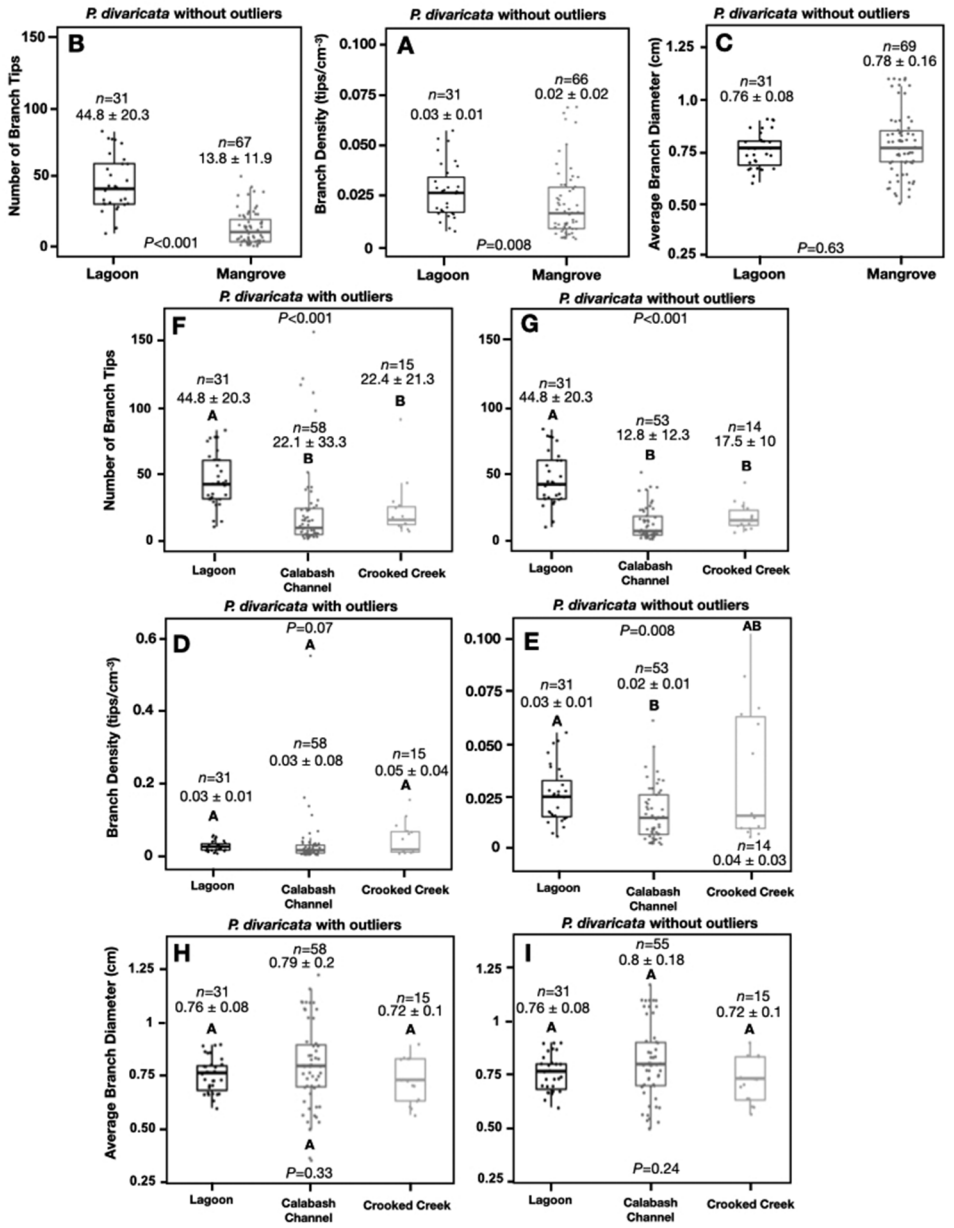

Figure A5. Boxplots depicting branch density, branch tip number, and average branch diameter in *Porites divaricata* in lagoon and mangrove environments when outliers were excluded (A, B, C, respectively) and when mangrove sites were separated, including (D, F, H, respectively) and excluding (E, G, I, respectively) outliers. The uppercase letters in (D)–(I) indicate that each of the three means is significantly different from the other two. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences in all three branch metrics between sites were determined with a Mann-Whitney-Wilcoxon test when mangrove sites were pooled and with Kruskal-Wallis and Dunn's tests when mangrove sites were separated.

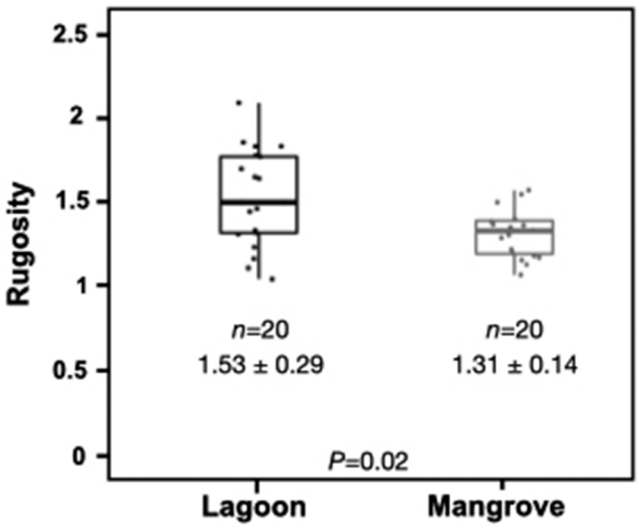

Figure A6. Boxplot depicting rugosity in *Porites astreoides* when outliers were excluded. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences in rugosity between sites were determined with a Mann-Whitney-Wilcoxon test.

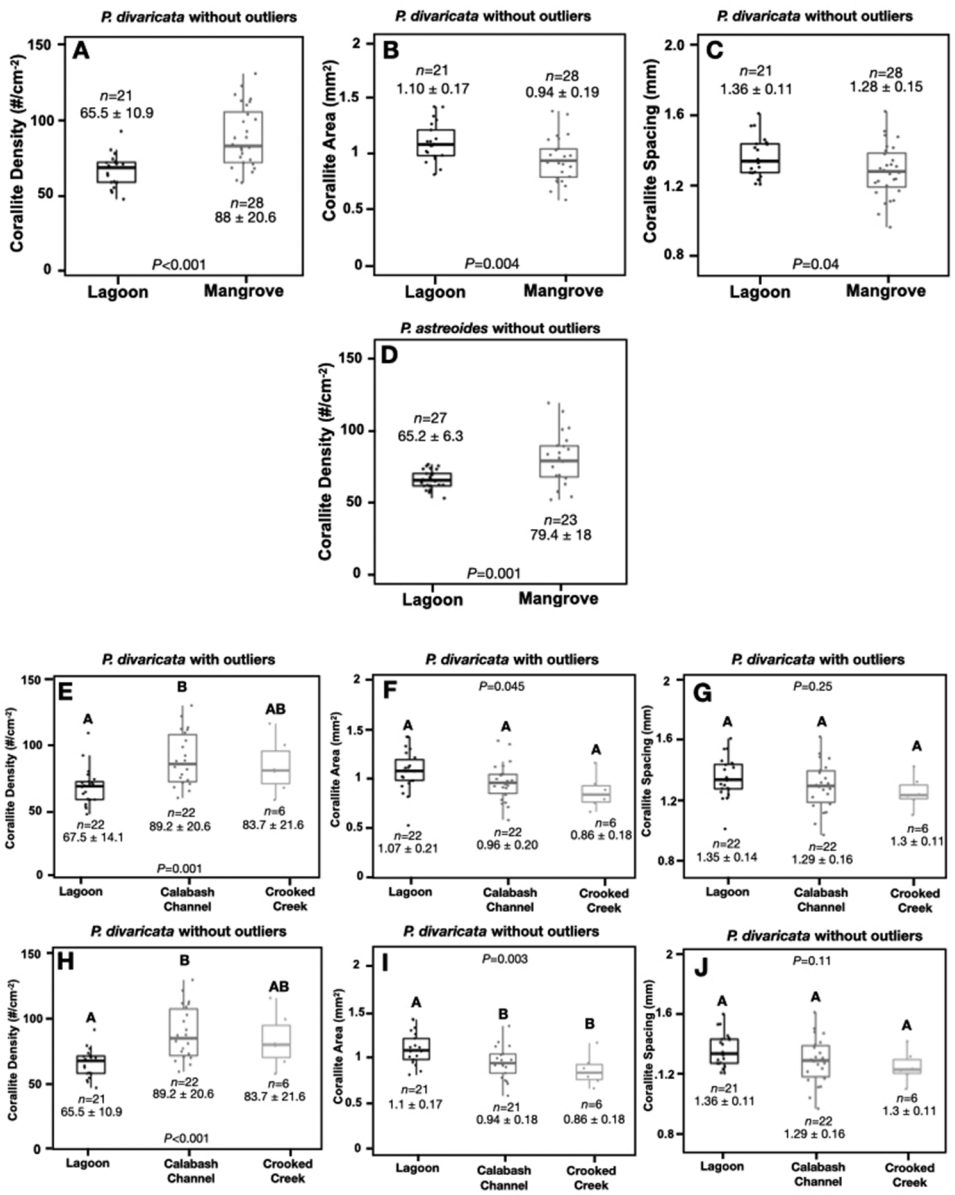

Figure A7. Boxplots depicting corallite density (A), corallite area (B), and corallite spacing (C) in *Porites divaricata* and corallite density in *Porites astreoides* (D) in lagoon and mangrove environments when outliers were excluded. The uppercase letters in (E)–(J) indicate that each of the three means is significantly different from the other two. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences in corallite density between sites were determined with a Mann-Whitney-Wilcoxon test in *P. divaricata* and a Welch two-sample *t* test in *P. astreoides*. Statistically significant differences in corallite area and spacing in *P. divaricata* were determined with a Student's two-sample *t* test. Boxplots depicting corallite density, corallite area, and corallite spacing in *P. divaricata* when mangrove sites were separated, both including (E–G) and excluding (H–J) outliers. Points, lines, and whiskers are as for (A–D). When mangrove sites were separated, statistically significant differences in corallite density were determined with Kruskal-Wallis and Dunn's tests when outliers were included and with an ANOVA and a Tukey *post hoc* test when outliers were excluded. Statistically significant differences in corallite area and spacing were determined with an ANOVA and a Tukey *post hoc* test both including and excluding outliers.

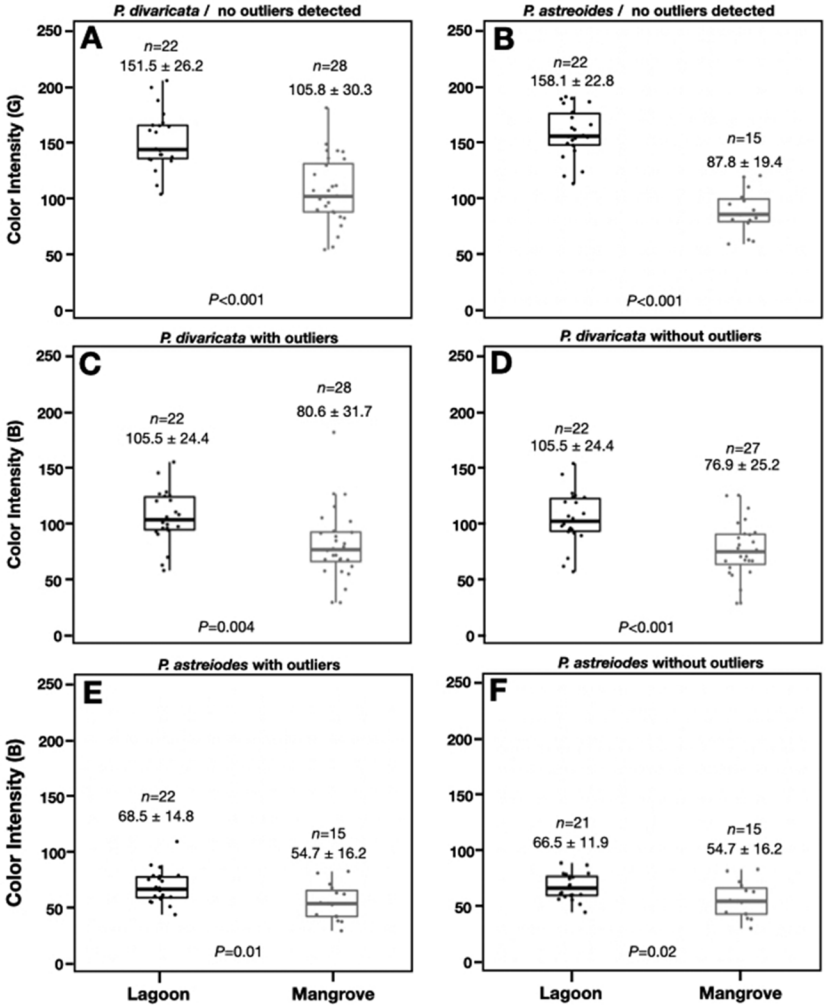

Figure A8. Color intensity of the green and blue channels in *Porites divaricata* and *Porites astreoides*. Mean color intensity in the green, G, color channel in *P. divaricata* (A) and *P. astreoides* (B) in which no outliers were detected. Mean color intensity in the blue, B, color channel in *P. divaricata* with (C) and without (D) outliers and in *P. astreoides* with (E) and without (F) outliers. Each point on the graph represents one colony. The line dividing the box into two sections represents the mean, the top and bottom lines of the box represent the interquartile range, and the whiskers represent the largest and smallest values that lie within 1.5 times the interquartile range. Statistically significant differences in colony color intensity in the green and blue channels between sites were determined with a Student's two-sample *t* test in both species.