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UNIVERSITY OF CALIFORNIA SAN DIEGO

Who's next door? Using GIS to understand neighbor patterns of coral and algae at Palmyra Atoll.

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Oceanography

by

Sarah A. McTague

Committee in charge:

Professor Stuart A. Sandin, Chair
Professor Jennifer Smith
Professor George Sugihara

2022

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The Thesis of Sarah A. McTague is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2022

DEDICATION

This work is entirely dedicated to my family, closest friends, and mentors, without whose constant support this thesis paper wouldn't have been possible. I especially have gratitude towards my parents and "siblings", Carol, Michael, Molly, and Paco McTague, for their words of encouragement and constant love during the hardships of graduate school. Thank you to my partner, Mitchell Chandler, for your help with everything from learning to code to thesis edits. More importantly, you are consistently there for me each day, and I am genuinely thankful for having you in my life. Thanks to friends Shelby Glasser, Michaela Omecinsky, Courtney King, Darren de Silva, Scott Carson, and Expedito Segovia for listening, talking me through complicated challenges, and making me laugh these past three years. Lastly, I want to thank my GIS mentors, Julie Wartell and Alihan Polat, who consistently inspire me every day and whose encouragement has led me to pursue a career I love.

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ABSTRACT OF THE THESIS

Who's next door? Using GIS to understand neighbor patterns of coral and algae at Palmyra Atoll.

by

Sarah A. McTague

Master of Science in Oceanography

University of California San Diego, 2022

Professor Stuart A. Sandin, Chair

The spatial distributions of benthic organisms within a coral reef ecosystem are structured by biological and physical mechanisms such as coral competition, reproduction, and reef structure. By examining the neighborhood patterns between scleractinian coral, soft coral, and algae, we can understand who typically lives near who and vice versa in a coral reef ecosystem. This brings insight into how organisms' interactions, life histories, and the reef's physical processes all impact the spatial distributions of colonies within their environment. Past coral spatial pattern studies relied on spatial point pattern (SPP) techniques such as

nearest neighbor analysis. SPPs utilize the centroid of a colony, which poorly represents benthic organisms due to their variability in shape and size. In this study, we used an in-situ imaging technique to produce 14 plots of the reef based around Palmyra Atoll, covering 1400 m² of benthic habitat in total. All colonies within these plots were identified to the lowest taxonomic classification possible. The utilization of GIS programming allowed us to take the shape of organisms into account and calculate the percent occupancy in 10 cm buffer regions around each colony. A bootstrapping approach was used to determine if the observed average neighborhood of each taxon and morphological type was more or less frequent compared to that of a null of equal occupancy. Few significant co-occurrence patterns were found due to the high abundance of a few taxa and competition between colonies. Of those significant neighbor patterns found, most positive patterns were intraspecific and biologically driven (via competition, reproduction, and partial mortality), and negative patterns were interspecific and were habitat driven (via physical processes and structure of the physical environment).

INTRODUCTION

The coral reef ecosystem consists of numerous organisms relying on the finite resources that the environment provides. These finite resources lead to interactions between neighboring coral colonies competing over limited benthic space to reside, light for photosynthesis, and access to currents carrying food (Connell 1973, Jones et al. 1994, Chadwick & Morrow 2011).

Competition for space is a significant factor in structuring coral communities (Sheppard 1979, Bak et al. 1982, Jones et al. 1994, Loya 1999, Grillo et al. 2018). Coral spatial distribution is affected by interspecific aggression, which can lead to highly aggressive taxa forming monospecific clumps on the reef (Sheppard 1979) and their subsequent removal of heterospecifics that come within their neighboring space (Chadwick & Morrow 2011).

Mechanisms of interspecific aggression for scleractinian corals include sweeper tentacles, extruding mesenterial filaments, mucus deployment, overtopping, shading, and filling (Lang 1971, Lang 1973, Connell 1973, Richardson et al. 1979, Wellington 1980, Bak et al. 1982, Rinkevich & Loya 1985, Chadwick & Morrow 2011).

Scleractinian intraspecific interactions also include aggressive behavior; however, they more often consist of skeletal fusion, growth stoppage at the contact of colonies, or growth around one another (Lang 1971, Lang 1973). Beneficial outcomes from these intraspecific interactions include an increase in survival of coral due to physical support and stabilization provided by the abutting of colonies (Chornesky 1991, Chadwick & Morrow 2011), a refuge from aggressive heterospecifics via monospecific clumping (Highsmith 1982, Cornell & Karlson 2000), and an increase in survival due to body size growth via fusion of separate colonies (Chadwick & Morrow 2011). Understandably then, intraspecific interactions play a minor role in

coral competition compared to interspecific interactions (5% versus 95% respectively) (Van Veghel et al. 1996).

Unlike scleractinian coral, soft corals lack stinging nematocysts and mesenterial filaments (Sammarco et al. 1985). Therefore, aggression by soft corals instead includes behaviors such as overgrowth, allelopathy, and whole-colony movement (Coll et al. 1982, Sammarco et al. 1983, Sammarco et al. 1985, Griffith 1997, Chadwick & Morrow 2011). During interactions between scleractinian and soft corals, scleractinians typically face partial or full mortality while soft corals face little to zero deleterious effects (Sammarco et al. 1983, Griffith 1997). Aggressive mechanisms of soft corals typically operate within 10 cm around the colony (Sammarco et al. 1983, Griffith 1997). Colonies of scleractinian corals *Porites cylindrica* (Dizon & Yap 2005), *Pavona cactus*, and *Goniastrea sp.* (Sammarco et al. 1983) found within this distance of soft coral colonies were previously studied. Observations from these studies found that adverse effects of soft coral aggression included growth rate stunts and local mortality in these scleractinian colonies. Competition between soft coral colonies exists; however, total colony reorientation typically occurs as an avoidance strategy instead (La Barre et al. 1986).

Other processes can also impact the spatial distribution of coral within their environment. Depending on a coral taxa's reproductive type, the larvae's dispersal can range from settlement next to their parent to a different reef kilometers away (Richmond & Hunter 1990, Carlon & Olson 1993, Miller & Mundy 2003). This vast difference could influence whether the coral taxa distribution is more clumped or dispersed within their environment. Taxa that perform fragmentation or partial mortality cluster more than taxa that do not (Highsmith 1982, Edwards et al. 2017). Diversity in the structure of the reef environment encourages niche partitioning, forcing the distribution of certain species to specific areas where heterospecifics do not reside

(Cornell & Karlson 2000). Physical processes of all sizes also impact coral spatial distributions. Regular wave action can drive detached solitary colonies into aggregations on the benthos (Chadwick-Furman et al. 1992), and large physical disturbance events can decrease coral densities and lower interspecific competition (Connell & Karlson 2000).

Therefore, competition, reproduction, partial mortality, physical processes, morphological types, and the environment's structure can all impact coral's spatial distribution. A specific focus on the neighborhood patterns of corals will bring further insight into how 1) coral interactions, 2) coral life histories, and 3) the impact of the physical environment on coral all impact the spatial distributions of colonies within their environment.

Most published studies of neighborhood patterns within benthic ecology have typically relied on spatial analyses adapted from terrestrial habitat studies (e.g. Turner 1989). One of the more frequently utilized spatial analysis techniques is spatial point patterns (SPP), such as nearest neighbor analysis, which relies on the centroids of organisms to examine their spatial patterns within the environment (Clark & Evans 1954). However, nearest neighbor analysis is less likely to find significant patterns compared to complex analyses such as buffer measures (Moilanen & Nieminen 2002). Furthermore, benthic organisms' geometries may be poorly represented by their centroid. As such, SPP techniques have limited use in understanding the direct neighborhood compositions of coral colonies.

However, few published studies have analyzed coral colony neighborhood patterns via a buffer measure. These few studies discovered that only a minority of coral taxa exhibited significant co-occurrence patterns within their environment. Of the significant co-occurrence patterns found, most negative associations were interspecific (100% in Bradbury & Young 1983 and 77% in Reichelt & Bradbury 1984), and most positive associations were intraspecific (75%

in Reichelt & Bradbury 1984). Studies examining coral spatial patterns without buffer measures also observed similar results (Rinkevich & Loya 1985, Chornesky 1991). All of these earlier studies may be hindered by a reliance on belt transects which only cover a small area of reef habitat, and a lack of understanding of the differences between observations of one colony or several colonies of the same taxa.

This limited examination of coral co-occurrence patterns means that most of our knowledge relies on published studies evaluating coral interactions without a specific focus on coral spatial patterns. Such studies exhibit either a heavy reliance on tank experiments (Lang 1973, McCook et al. 2001) or on manipulating coral placement within the environment if conducted in the field (Richardson et al. 1979, Sammarco et al. 1983, Sammarco et al. 1985, Van Veghel et al. 1996). Observing naturally occurring neighbor interactions via these lab-based or manipulative field experiments is impossible.

Recent developments in digital imagery have greatly improved our ability to analyze marine benthic environments. Specifically, large-area imagery stitches thousands of images of reef habitat into one photomosaic (e.g., Fig. 2a) that can cover hundreds to thousands of square meters (Gracias et al. 2003, Lirman et al. 2007). These photomosaics are incredibly detailed, allowing for thousands of individual colonies to be traced and identified down to the species level. The utilization of detailed photomosaics can determine if one is observing one colony or several colonies of the same species. Acquisition of data via imagery also allows lab-based analyses to follow, including colony-level spatial patterns (Edwards et al. 2017, Pedersen et al. 2019). This technique allows for the analysis of the marine benthos without directly manipulating the environment.

In this study, we analyze neighborhood compositions and co-occurrence patterns of taxa and morphological types at Palmyra Atoll (Fig. 1). We are specifically interested in how each taxon and morphological type live in proximity to one another, possibly creating distinct neighborhood compositions for each colony found in the reef environment. Data are collected via large-area imagery and transformed into digitized photomosaics which map out individual colonies from 14 sites of reef habitat (1400 m² of area). Using large-area imagery allows us to (1) examine reef habitat on a larger scale compared to previous neighborhood composition studies and (2) create neighborhood buffer spaces around all individual colonies using the distinct shape of each organism. We use ArcGIS programming to develop neighborhood buffer areas around each colony and calculate the percent area colonies occupy within each buffer space. We examine the co-occurrence patterns between each coral taxa and morphological type pairing and discuss the natural ecological processes that produce these patterns.

METHODS

2.1 Study Locations

Data were collected on Palmyra Atoll (5°52'N, 162°06'W; Fig. 1), a US Fish and Wildlife National Wildlife Refuge based in the northern Line Islands. Located in the central Pacific, the atoll is located approximately 1,700 kilometers South-West of Hawai'i and 2,400 kilometers North-East of American Samoa. The atoll comprises two inner lagoons and an outer fore-reef characterized by steep slopes, high coral cover, and good water visibility (Papastamatiou et al. 2010).

Other than during World War II, when the United States military occupied the atoll, Palmyra has never held a permanent population (Dawson 1959, Papastamatiou et al. 2010).

Therefore, due to the lack of anthropogenic impacts and its remote location, Palmyra is a near-pristine reef that sustains a healthy coral population, high apex predator biomass, and sizeable total fish biomass (Stevenson et al. 2007, Sandin et al. 2008).

Fourteen 10x10 meter sites have been established on the north and south sides of the atoll (Fig. 1). Each site is at a depth of approximately 10 meters, with the corners of each site marked using stainless steel stakes. Sites are located approximately every 1 kilometer along the coastline to obtain broad spatial coverage while ensuring spatial independence between sites.

2.2 Photomosaic Collection

Authors utilized large-area image reconstruction to survey all fourteen sites in September 2013. A diver collected imagery using a camera system consisting of two Nikon D7000 16.2-megapixel DSLR cameras mounted on a custom frame. One camera used a wide-angle lens set to an 18mm focal length to establish overlap between bordering images. The second camera used a 55mm focal length lens to obtain higher resolution imagery for taxonomic classifications. The diver swam approximately 1.5m above the substrate in a gridded pattern across each site, ensuring approximately 90% overlap between successive passes. Cameras were programmed to capture one image per second using built-in intervalometers and gathered 2500 images per site on average.

2.3 Imaging Processing

To form spatially continuous images of each site, two-dimensional composite mosaics were created from the thousands of individual images taken from Palmyra Atoll using previously described image recognition algorithms (Gracias et al. 2003, Negahdaripour & Madjidi 2003,

Lirman et al. 2007). In this process, raw images were fused using image processing and numerical optimization modules that work with little user intervention to create finalized mosaics (Fig. 2a).

All photomosaics were further processed via a manual digitization methodology that was adapted from previous work (Lirman et al. 2007). Images were uploaded to Adobe Photoshop CC, and boundaries of live colonies $> 9 \text{ cm}^2$ (the minimum size of an adult-sized colony) were digitized by hand using a Walcom pen-tablet (model #CTH-470) (Fig. 2b). Individual colonies were determined using the operational definition that defines a colony as a continuous patch of live tissue (Highsmith 1982). The best available species list (Table S1) was used to classify corals and algae to the highest taxonomic classification possible. All colonies of the same taxonomic classification were filled in with a set color, then represented by an image layer in Photoshop and exported as a PNG file. This was repeated for each taxonomic classification found within each site. Exported image files were then processed using the ArcGIS desktop application ArcGIS Pro. Each PNG file of a taxonomic classification was uploaded into ArcGIS Pro as a raster surface and converted into a vector polygon layer using the *Raster to Vector* tool (Fig. 2c). A selection was further run on all vector polygons to guarantee only colonies $> 9 \text{ cm}^2$ were included in the analysis.

Next, the *Buffer* tool in ArcGIS Pro was utilized to create distinct neighborhood buffers for each colony with a distance $d = 10 \text{ cm}$ (Fig. 3). This distance was selected because (1) it is the extent to which aggressive defense mechanisms of corals (such as sweeper tentacles) can typically reach (Sammarco et al. 1983, Griffith 1997, Lapid et al. 2004, Dizon & Yap 2005), and (2) past studies focused on coral neighborhood patterns utilized this distance (Bradbury & Young 1983, Reichelt & Bradbury 1984). To ensure accuracy in assessing the neighborhood

composition of each buffer, the *outside_only* function of the buffer tool was applied so that buffers were generated only outside the colony polygons, and the area made up by the colony polygons was erased from the output buffer. To avoid any edge effect, only buffers completely contained within the borders of the mosaic were included. However, all colonies residing within the mosaic remained in the analysis regardless of if their buffer was cut.

2.4 Statistical Analysis

After all neighborhood buffers were constructed, the *Tabulate Intersection* analysis tool in ArcGIS Pro was used to calculate the percent area of each neighborhood buffer intersected by a neighboring colony. When multiple colonies of different taxonomic classifications intersected a neighborhood buffer, the percent area each taxon took up within the buffer space was calculated and reported separately. Whereas when a neighborhood buffer was intersected by multiple colonies of the same taxonomic classification, a single calculated percent area was reported representing the total area all colonies took up within that buffer space. All data were converted into ratios and labeled with the taxonomic classifications of the neighborhood buffer colony and neighboring colony found within the buffer space. In Figure 3, an example taxa pairing would include *Pocillopora* (neighborhood buffer colony) and *Fungia* (neighboring colony found in the buffer space of *Pocillopora*).

We then assessed if the taxa pairing ratios were due to random or determined processes. Ratios of each taxa pairing within the given site were averaged. In instances where a taxon was not found in the neighborhood buffer area of another, although both taxa were present in the site, the ratio of that taxa pairing was 0. We produced null distributions of the taxon's buffer composition using a bootstrapping approach to determine if an average ratio was statistically

different from the corresponding null distribution. First, in the bootstrapping approach, random ratio samples were taken with repetition from the entire population regardless of classification and averaged. The number of samples was equivalent to the taxon's buffer count within the given site. This process was repeated 10000 times to create the null distribution for the given taxon. This was then repeated for each taxon found in the site. The whole process was completed analytically using custom algorithms designed by the authors via R 3.6.2 (R Core Team 2018).

We then compared the average ratio for each taxa pairing to the null distribution of the neighborhood buffer taxon within the pairing. Values above the 97.5 percentile of the null distribution indicated a positive co-occurrence between the two taxa within that pairing (i.e., the taxa were neighbors more often than could be attributed to randomness). Values below the 2.5 percentile indicated a negative co-occurrence (i.e., the taxa were not neighbors more often than could be attributed to randomness). Values between the 2.5 and 97.5 percentile indicated a co-occurrence pattern that was random and non-significant.

This entire statistical analysis was repeated for each site. A multinomial test tested for statistically significant differences between the number of sites where each of the taxa pairings had positive co-occurrences, negative co-occurrences, and non-significant co-occurrences. The strength of significant co-occurrences (positive and negative) were determined based on an algorithm of $(\text{Number of Positive Sites} - \text{Number of Negative Sites}) / (\text{Total Sites})$. The complete analysis over all 14 sites was rerun without algae (*Caulerpa*, *Dictyosphaeria*, *Halimeda*, & *Lobophora variegata*) and *Fungia* to confirm that highly abundant algae or solitary taxa did not dilute co-occurrence signals within the initial analysis.

Taxa were then sorted into functional morphology groups. The previous process was replicated to determine if the neighborhood of each colony was specific to its functional morphology within a given distance d . Colonies were grouped by similar functional morphology via the *Merge Tool* in ArcGIS Pro. Morphology classifications were algae, branching, corymbose, digitate, encrusting, foliose, massive, plating, soft, solitary, submassive, and tabulate (Table S1).

2.5 Succession Analysis

We utilized methodology from McNamara et al. 2019 to understand if the differences in non-random patterning between sites were due to individual successional levels. This method uses spatial forecasting to understand the nonlinear dynamics of a coral reef ecosystem. Those sites with spatial determinism were in an intermediate successional stage, and those with spatial randomness were in the early or late stages of succession. The reader is referred to McNamara et al. 2019 for complete details.

RESULTS

3.1 Colony Abundance

49318 individual colonies ($> 9 \text{ cm}^2$) from 52 different taxonomic groups and 12 different morphological types were traced and identified in 1400 m^2 of reef habitat. Total colony abundance within a site ranged from a minimum of 2466 colonies (FR7) to a maximum of 5780 (FR9) and with an average of 3523 ± 227 (mean \pm SE) colonies per site (with each site covering 100 m^2).

Porites superfusa was the most abundant taxon with an average of 712 +/- 100 colonies per 100 m² site (mean +/- SE) and made up 20.2% of all traced colonies across all sites (Fig. 4). *Halimeda* was the second most abundant taxon with an average of 678 +/- 55 patches per 100 m² site and made up 19.2% of all traced (Fig. 4). The third most abundant taxon was *Fungia* with an average of 389 +/- 157 colonies per site and made up 11.1% of all traced (Fig. 4). *Fungia* also displayed the most considerable variability between sites, with abundance ranging from 22 colonies (FR36) to 1949 (FR9). Other central taxa in decreasing abundance included *Pocillopora*, *Montipora* (encrusting), *Goniastrea stelligera*, and *Porites* (massive) (Fig. 4). Colonies of the 20 least abundant taxa accounted for less than 1% of all traced colonies.

Encrusting was the most abundant morphological type with an average of 1161 +/- 93 colonies per 100 m² site (mean +/- SE) and made up 33% of all traced colonies (Fig. 5). The second most abundant morphology was algae with an average of 684 +/- 70 patches per 100 m² site and made up 19.4% of all traced (Fig. 5). Solitary was the third most abundant morphological type with an average of 392 +/- 157 colonies per 100 m² site and made up 11.1% of all traced (Fig. 5). Solitary (made up of taxa *Fungia* and *Halomitra*) also displayed the most considerable variability between sites of all morphologies, ranging from an abundance of 22 colonies (FR36) to 1949 (FR9). Other central morphologies in decreasing abundance included corymbose, submassive, massive, soft, and plating (Fig. 5). Colonies of the remaining morphologies (foliose, branching, tabulate, and digitate) accounted for less than 1.5% of all traced colonies.

3.2 Taxa Analysis

Multinomial tests were used to test for statistically significant differences between the number of sites where each of the taxa pairings had experienced positive co-occurrences, negative co-occurrences, and non-significant co-occurrences. In the taxa analysis, 30 out of a possible 2704 (1.12%) patterns of co-occurrence between taxa pairings had p-values less than 0.05 and were considered significant (Table 1).

21 out of 30 (70%) significant co-occurrences were positive (where taxa neighbored one another more often than could be attributed to chance). Of those positive co-occurrences, 17 (80.95%) were intraspecific and involved the following taxa: *Stylophora*, *Porites superfusa*, *Montipora* (encrusting), *Fungia*, *Dictyosphaeria*, *Pachyclavularia*, *Echinopora*, *Pavona chiriquiensis*, *Pavona* (submassive), *Zooanthid*, *Goniastrea stelligera*, *Favites* (encrusting), *Leptastrea*, *Montipora* (plating), *Acropora* (corymbose), *Porites* (massive), and *Favites* (submassive) (Table 1). The remaining 4 (19.05%) positive co-occurrences were interspecific and consisted of co-occurrences of *Halimeda* with *Sinularia*, *Pachyclavularia*, and *Sarcophyton* (Table 1). The strongest four positive co-occurrences were intraspecific, involving *Stylophora*, *Porites superfusa*, *Montipora* (encrusting), and *Fungia* (Table 1).

The remaining 9 out of 30 (30%) significant co-occurrences were negative (where taxa were not neighboring one another more often than could be attributed to chance). Of these 9 negative co-occurrences, 8 (88.9%) were interspecific and involved the following taxa pairings: *Porites superfusa* with *Sinularia*, *Montipora* (encrusting), *Porites* (massive) & *Goniastrea stelligera*, and *Fungia* with *Sinularia*, *Pocillopora* & *Goniastrea stelligera*. The remaining negative co-occurrence was intraspecific (11.1%) with the taxon *Halimeda*. The strongest four

negative co-occurrences were all interspecific and involved *Porites superfusa* with *Sinularia*, *Montipora* (encrusting), & *Porites* (massive), and *Fungia* with *Sinularia* (Table 1).

Overall, 21 taxa were part of at least one significant ($p < 0.05$) co-occurrence pairing (positive or negative). These taxa all fell within the top 29 out of 52 most abundant taxa (Fig. 4) and made up 89.73% of total traced colonies. The taxon that was involved in the most significant co-occurrences was *Porites superfusa*, which was part of 6 significant co-occurrences, followed by *Halimeda* (5 significant co-occurrences), *Fungia* (4), *Sinularia* (4), *Porites* (massive) (3), *Goniastrea stelligera* (3), *Montipora* (encrusting) (2), and *Pachyclavularia* (2) (Fig. 6). These 8 were among the top 11 most abundant taxa and comprised 67.23% of total traced colonies.

There were 2674 (98.9%) non-significant ($p > 0.05$) co-occurrence patterns between taxa pairings. Taxa part of only non-significant co-occurrences comprised 10.27% of the total traced colony count.

The complete rerun of the analysis without algae or *Fungia* resulted in similar results (Table S2). Minor differences compared to the original taxa analysis included adding 3 positive and 2 negative co-occurrences, and removing 2 positive co-occurrences. Therefore, our approach is robust, and we can continue with the original taxa analysis within this study.

3.3 Morphological Analysis

In the multinomial tests on the morphologies, 15 out of a possible 144 (10.42%) patterns of co-occurrence between morphological pairings were significant ($p < 0.05$) (Table 2). Of these 15 significant pairings, 9 (60%) were positive. 5 of these 9 (55.6%) positive co-occurrences were intraspecific, involving solitary, plating, encrusting, submassive, and massive morphologies. The

remaining 4 (44.6%) positive co-occurrences were interspecific, consisting of co-occurrences of algae with soft, massive, & submassive. The strongest positive co-occurrence involved solitary, followed by plating, encrusting, and soft with algae tied for second (Table 2).

The remaining 6 out of 15 (40%) significant co-occurrence patterns were negative. Of these negative co-occurrences, 5 out of 6 (83.3%) were interspecific and consisted of co-occurrences of encrusting with soft, massive, & solitary, and corymbose with soft & solitary. The remaining negative co-occurrence was intraspecific (16.7%) between algae. The strongest 3 co-occurrences involved encrusting with soft & massive, and algae (Table 2).

Solitary, soft, algae, plating, encrusting, submassive, massive, and corymbose were all involved in at least one significant ($p < 0.05$) co-occurrence pairing. These morphologies were the top 8 most abundant and made up 99% of total traced colonies. The morphology that was involved in the most significant co-occurrences was algae, which was part of 5 significant co-occurrences, followed by encrusting (4 significant co-occurrences), soft (4), solitary (3), massive (3), submassive (2), and corymbose (2) (Fig. 7). These 7 morphologies made up 96% of total traced colonies.

129 (89.58%) non-significant ($p > 0.05$) co-occurrence patterns between morphological pairings were found. Morphologies involved in only non-significant co-occurrences made up 1.4% of the total traced colony count.

3.4 Succession Analysis

Sites FR3, FR4, FR9, FR36, FR38, FR39, and FR40 were spatially random and thus in early or late levels of succession. All but two of these sites are on the south side of the atoll

(Fig.8). Sites FR7, FR8, FR13, FR14, FR37, FR69, and FR132 had nonlinear spatial determinism and thus in intermediate levels of succession. All these sites are located on the north side of the Atoll (Fig. 8).

Percent cover of *Halimeda*, *Sinularia*, *Sarcophyton*, *Pachyclavularia*, and *Zooanthid* varied between sites of nonlinear spatial determinism and spatial randomness. The average percent cover of *Halimeda* per site was higher in those of nonlinear spatial determinism (16.49%) than those of spatial randomness (9.35%). This is the same for *Sinularia* (11.45% versus 2.69%), *Sarcophyton* (4.61% versus 1.93%), *Pachyclavularia* (1.04% versus 0.16%) and *Zooanthid* (0.17% versus 0.07%).

DISCUSSION

We explored the neighborhood patterns of scleractinian corals, soft corals, and algae of Palmyra Atoll coral reef in 2013. Specifically, we utilized a combination of spatial and statistical programming to examine what co-occurrence patterns emerged from taxa and morphological pairings across all 14 sites. Our analyses found few significant co-occurrence patterns (Tables 1 and 2). These results are supported by previous studies (Bradbury & Young 1983, Reichelt & Bradbury 1994). Most co-occurrence patterns were non-significant due to the high abundance of a few specific taxa and competition between coral colonies.

In this study, most of the significant positive co-occurrences were intraspecific, and significant negative co-occurrences interspecific (Tables 1 and 2). Previous coral neighbor pattern studies had found positive interactions were primarily between conspecifics and negative interactions between heterospecifics (Bradbury & Young 1983, Reichelt & Bradbury 1994). Specifically, conspecifics of various coral taxa and morphological types have displayed

aggregative spatial patterns (Rinkevich & Loya 1985, Chornesky 1991, Chadwick & Morrow 2011, Edwards et al. 2017). The results of this study could be attributed to a few factors, including but not limited to competition, reproduction, partial mortality, preference of location on the reef, physical processes, and the structure of the physical environment (Highsmith 1982, Bradbury & Young 1983, Reichelt & Bradbury 1984, Edwards et al. 2017). All significant positive co-occurrences were biologically driven (via competition, reproduction, and partial mortality), and all significant negative co-occurrences were habitat driven (via physical processes and structure of the physical environment).

4.1 Colony Abundance

In the taxa analysis, the top three most abundant taxa (*Porites superfusa*, *Halimeda*, and *Fungia*) were involved in the greatest number of significant co-occurrences out of all taxa within the analysis (Fig. 6). All taxa that were involved in at least one significant co-occurrence (*Porites superfusa*, *Halimeda*, *Fungia*, *Pocillopora*, *Montipora* (encrusting), *Goniastrea stelligera*, *Porites* (massive), *Pavona chiriquiensis*, *Sinularia*, *Pachyclavularia*, *Pavona* (submassive), *Echinopora*, *Stylophora*, *Sarcophyton*, *Favites* (encrusting), *Dictyophaeria*, *Montipora* (plating), *Favites* (submassive), *Zooanthid*, *Leptastrea*, and *Acropora* (corymbose)) together made up the total abundance of over 90% of traced colonies. In the morphological analysis, the top three most abundant morphologies (encrusting, algae, and solitary) were involved in the top four greatest number of significant co-occurrences out of all morphologies (Fig. 7). All morphological types that took part in at least one significant co-occurrence (encrusting, algae, solitary, corymbose, submassive, massive, soft, and plating) together made up the total abundance of 98.6% of colonies.

Those taxa involved in only non-significant co-occurrences were on average lower in abundance than those involved in at least one significant co-occurrence (12 versus 158 average colonies per 100 m² site respectively). From the taxa analysis, only taxa *Astrea curta*, *Hydnophora microconos*, *Pavona* (massive), and *Turbinaria* (all taxa types involved in only non-significant co-occurrences) individually had mean abundance counts per 100 m² site that fell within the abundance distribution of those taxa types that were involved in at least one significant co-occurrence (Fig. 4). This is excluding taxon *Acropora* (corymbose), which although part of one significant co-occurrence, was on average 147 colonies per 100 m² site lower in abundance than all other taxa types present in at least one significant co-occurrence.

Similarly, in the morphological analysis, morphologies involved in only non-significant co-occurrence patterns were on average lower in abundance than those involved in at least one significant co-occurrence (12 versus 424 average colonies per 100 m² site respectively). From the morphological analysis, zero morphological types involved in only non-significant co-occurrences fell within the abundance distribution of those morphologies involved in at least one significant co-occurrence. (Fig. 5).

In previous neighbor pattern studies, individual taxa were significantly more abundant in transects/sites where they were also involved in significant neighbor adjacencies (Reichelt & Bradbury 1984, Grillo et al. 2018). Therefore, only those taxa and morphological types high enough in abundance in the Palmyra Atoll reef environment are part of significant positive or negative co-occurrence patterns.

4.2 Competition

Interspecific competition is when two colonies of differing taxa aggressively interact with one another to gain a necessary resource. One or both coral colonies may face deleterious effects due to this interaction. For scleractinian corals, mechanisms of interspecific aggression include sweeper tentacles, extruding mesenterial filaments, mucus deployment, overtopping, shading, and filling (Lang 1971, Lang 1973, Connell 1973, Richardson et al. 1979, Wellington 1980, Bak et al. 1982, Rinkevich & Loya 1985, Chadwick & Morrow 2011). Elongated sweeper tentacles can push away nearby recruits and established adults within reach, protecting the colony and maintaining space within their neighboring area. Large coral colonies have space around them, most likely created by this aggressive mechanism which allows them to defend space effectively and persist as large and long-lived corals (Chadwick & Morrow 2011).

During interspecific competition, soft corals utilize overgrowth, whole-colony movement across neighboring scleractinian corals, and allelopathy (Sheppard 1979, Coll et al. 1982, Sammarco et al. 1983, Sammarco et al. 1985, Griffith 1997, Chadwick & Morrow 2011). Allelopathy is the direct inhibition of one species by another using toxic chemicals (Sheppard 1979). Soft corals utilize allelochemicals in several ways within the neighboring space around their established colony. These include killing colonies of competing corals, reducing encroachment of competitors, inhibiting heterospecific larval metamorphosis, and killing heterospecific swimming larvae that pass by (Maida et al. 1995, Atrigenio & Alino 1996, Griffith 1997, Chadwick & Morrow 2011). Soft corals can retain and release allelochemicals as need be. Certain soft corals utilize allelopathy only when they need to protect themselves from incoming predators. In contrast, others utilize it as a mechanism to maintain living space by creating a “halo of toxins” that prevents other corals from encroaching into their neighboring

space (Sheppard 1979, Coll et al. 1982, Sammarco et al. 1983, Sammarco et al. 1985, La Barre et al. 1986). Therefore, scleractinian corals face mortality during direct and non-direct contact with soft coral.

The distance in which aggressive mechanisms can reach varies between scleractinian corals and soft corals. Scleractinian coral mechanisms such as mesenterial filaments can extend up to 5 cm (Dustan 1975, Bak et al. 1982) and sweeper tentacles up to 6.5 cm (Richardson et al. 1979, Sebens & Miles 1988, Langmead & Chadwick-Furman 1999, Lapid et al. 2004), with mechanism reach dependent on taxa type. Soft corals differ due to their heavier use of allelopathy. Previous studies have found that scleractinian corals within 10-15 cm of a soft coral displayed signs of local mortality (Dizon & Yap 2005, Griffith 1997, Sammarco et al. 1983). However, there have been observations of deleterious effects on scleractinians from soft corals up to 30 cm away (Sammarco et al. 1983). The use of allelopathy varies between soft coral species, with *Sinularia* and *Sarcophyton* being of utmost toxicity (Coll et al. 1982, Sammarco et al. 1983). With all this in mind, aggressive mechanisms of both scleractinian and soft corals can reach a great extent of the 10 cm neighborhood buffer used within this study.

Overall, interspecific aggression leads to multiple possible outcomes, including (1) partial/total mortality of coral larvae, juveniles, or established colonies participating in an interaction, (2) reorientation of one or both colonies after an interaction, and (3) the complete exclusion of colonies from ever entering the neighboring space of a coral. Interspecific interactions of scleractinian and soft corals can occur within the distance of the neighborhood buffers utilized in this study. Therefore, the high presence of interspecific aggression within the Palmyra Atoll reef environment has led to zero positive interspecific co-occurrences between corals in this study's taxa and morphological analyses (Tables 1 and 2). It is important to note

that within this study, only live coral was traced and processed via our methodology. Coral death could result from many things, including competition, and dead coral sections were not included in the neighborhood compositions of colonies within our analyses. Therefore, competition that resulted in the death of coral within the neighborhood boundary of another live colony would support our finding of no positive interspecific co-occurrences between corals within the results.

Co-settlement and aggregation of conspecifics may lead to intraspecific competition, which is when two colonies of the same taxa aggressively interact with one another. Intraspecific aggression includes physical actions such as skeletal overgrowth, retreat growth, and nematocyst discharge (Rinkevich & Loya 1985, Chadwick & Morrow 2011). This form of competition is less deleterious to participants and does not occur as frequently as interspecific competition.

In some instances, there is a complete lack of aggressive behavior between conspecifics. Conspecific scleractinian coral that settle next to one another will stop growing in the region of contact, continue to grow but around one another, or fuse their adjacent tissue or skeletons (Lang 1971, Lang 1973). This lack of aggression was observed when conspecifics were transferred to the same habitat from different geographic locations, and zero aggressive behavior followed between the colonies (Lang 1971). The fusion or the abutting of coral colonies leads to an increase in survival due to an increase in colony size and physical stability (Chornesky 1991, Chadwick & Morrow 2011). Soft coral intraspecific interactions lead to competition; however, total colony reorientation typically transpires instead as an avoidance strategy (La Barre et al. 1986). Furthermore, soft coral allelochemicals kill heterospecific coral larvae but not conspecifics (Chadwick & Morrow 2011).

There is generally less aggression between coral conspecifics in comparison to heterospecifics. This lack of intense aggression between conspecific corals is partially why many positive co-occurrences were intraspecific in this study's taxa and morphological analyses (Tables 1 and 2).

Along with the abundance levels of colonies at Palmyra Atoll as discussed earlier, competition is why we are observing a large majority of the co-occurrence patterns to be non-significant. The combination of coral interspecific and intraspecific competition means many coral colonies are not frequently within the neighborhood space of other specific taxa/morphological types enough to produce significant neighborhood co-occurrence patterns.

4.3 Reproduction

There are multiple ways coral taxa can sexually reproduce, including broadcast spawning and brooding. Broadcast spawning is the release of gametes into the water column where fertilization occurs externally (Harrison et al. 1984, Shlesinger & Loya 1985, Richmond & Hunter 1990). Larvae remain in the water column for days to weeks to disperse offspring into new reef territory kilometers away. This larvae suspension decreases competition between parents and offspring, and increases genetic diversity (Babcock & Heyward 1986, Miller & Mundy 2003, Glynn et al. 2017). Brooding is the fertilization of gametes internally, and larvae are released once they are relatively developed (Richmond & Hunter 1990, Carlon & Olson 1993, Isomura & Nishihira 2001). The larvae dispersal distance is much shorter than broadcast spawning (less than 1 kilometer) (Gilmour et al. 2016). Coral taxa that utilize similar reproductive types may still differ in their larvae dispersal distances due to differences in settlement preference and their respective larvae's swimming ability (Carlon & Olson 1993).

Differences in sexual reproduction and dispersal of offspring could lead to contrasts in coral taxa spatial patterns. Those taxa that rely on brooding over broadcasting and whose larvae cannot swim as long could lead to more intraspecific neighbor compositions as their larvae are more likely to end up near the parent colony. However, we believe that sexual reproduction has far less of an impact on spatial distributions of coral colonies than asexual reproduction. In previous work, juvenile corals showed random spatial patterning in relation to adults, suggesting that adult spatial patterns are driven more heavily by processes such as asexual reproduction via fragmentation and partial mortality (Pedersen et al. 2019).

Fragmentation is a coral colony's ability to split into multiple viable colonies via storms and waves, bioerosion, and corallivory (Highsmith 1982, Cornell & Karlson 2000, Glynn et al. 2017). This process significantly affects the local distribution of coral colonies within their environment. It leads to an aggregation of conspecifics because larger-sized fragments tend to remain near the parent where the environment is predictable, and the mortality rate is lower (Highsmith 1982, Boller et al. 2002). These monospecific coral thickets lead to high growth rates, and avoidance of reef-bound competitors (Highsmith 1982).

Partial mortality is the loss of part of the living tissue of a coral organism via a stress event such as disease, predation, or partial bleaching (Meesters et al. 1996, Lirman 2000, Furby et al. 2017). Because corals are colonial organisms made up of hundreds to thousands of interconnected polyps, they can survive this partial damage (Richmond 1997). The lesion will grow inward to recover the wound. However, if this fails, it will remain permanent and be displayed as a bare patch of skeleton on the surface of a colony (Bak & Steward-Van Es 1980, Meesters et al. 1996). Unlike fragmentation, this does not result directly in splitting a colony skeleton and creating multiple colonies from one (Highsmith 1982), as seen with asexual

fragmentation. However, the weakening of the skeleton along a lesion may eventually lead to the subdivision into identical daughter colonies via storm damage or the boring of organisms taking advantage of open skeleton space (Highsmith 1981). Permanent partial mortality may also lead to colonization by other organisms, such as algae within the coral's lesion (Pinon-Gonzalez & Banaszak 2018). In our results, morphology algae has positive interspecific co-occurrences with morphologies massive and submassive in the morphology analysis (Table 2). Algae colonization of lesions from partial mortality could have a part in these patterns.

The morphologies of those coral taxa that fragment include branching (Highsmith 1982, Wallace 1985), encrusting (Pedersen et al. 2019), plating (Work & Aeby 2011), massive and submassive (Highsmith 1982, Foster et al. 2007). These four morphologies also exhibit partial mortality (Meesters et al. 1996, Lirman & Fong 1997, Shenkar et al. 2005, Bruckner & Dempsey 2015, Kenyon et al. 2020). Scleractinian taxa such as *Porites* (Glynn et al. 2017, Furby et al. 2017), *Montipora* (Heyward & Collins 1985), *Pavona* (Highsmith 1982, Glynn et al. 2017), *Stylophora* (Rinkevich & Loya 1985), *Acropora* (Wallace 1985, Lirman 2000), *Leptastrea* (van Woesik et al. 2011), *Favites* (Edwards et al. 2017), *Goniastrea* (van Woesik et al. 2011), and *Echinopora* (Bak & Meesters 2000) utilize fragmentation. Likewise, these nine taxa exhibit partial mortality (Lirman & Fong 1997, Yamashiro et al. 2000, Glynn et al. 2000, Wesseling et al. 2001, Obura 2001, McClanahan et al. 2004, van Woesik et al. 2011, Brown & Phongsuwan 2012, Horoszowski-Fridman et al. 2015). All morphologies listed above and taxa *Porites*, *Montipora*, *Pavona*, *Acropora*, *Stylophora*, and *Favites* have displayed clustering patterns in previous work (Edwards et al. 2017).

Fungia (which comprises 99.6% of colonies that fall within the solitary morphology) have a dual mode of asexual reproduction that leads to clumps of adults originating from one

larva. *Fungia* colonies are initially connected via a stem to the substrate; after they are released, the stem may survive and generate more polyps (Highsmith 1982). The detached polyp may also produce new polyps on its skeleton, which will detach from the parent (Gilmour 2004). This process is called budding and is another form of asexual reproduction which leads to monospecific clumping. *Fungia* colonies have displayed partial mortality as well (Chadwick-Furman et al. 2000). In Edwards et al. (2017), taxa *Fungia* and morphology solitary displayed some of the greatest clustering patterns of all taxa and morphology analyzed within the study.

All taxa and morphology listed above due to their ability to perform asexual reproduction and partial mortality were in positive intraspecific co-occurrences in this study. Both processes lead to monospecific aggregative patterns and higher abundance levels (Highsmith 1982). Therefore, the heavy presence of fragmentation and partial mortality at Palmyra Atoll has partially driven our results' positive intraspecific co-occurrences (Tables 1 and 2).

4.4 Structure and physical forcings of the reef environment

By utilizing the diverse structure of the reef environment, certain taxa and morphologies live in specific locations within the reef not inhabited by heterospecifics. This partitioning has led to multiple interspecific negative co-occurrences in this study's taxa and morphological analyses (Tables 1 & 2). *Fungia* is a solitary coral that lives on unstable substrates such as sand (Hoeksema & Moka 1989, Kramarsky-Winter & Loya 2000). Because *Fungia* is unattached to the reef substrate, colonies are deposited to specific locations on the benthos via physical processes such as waves and water currents (Edwards et al. 2017). Therefore, solitary colonies of *Fungia* are typically found in large monospecific aggregations (Wells 1966, Rosen & Taylor 1969, Sheppard 1981, Chadwick & Morrow 2011), as displayed in imagery from sites at Palmyra

Atoll (Fig. 9). Consequently, *Fungia* in the taxa analysis and solitary in the morphological analysis have positive intraspecific co-occurrences (Tables 1 & 2).

Non-solitary coral taxa are typically distributed vertically higher within the reef environment and on substrates such as calcareous rock, coral colonies, and rubble (a composition of dead coral pieces and fragmented reef rock) (Norstrom et al. 2007, Duckworth & Wolff 2011, Ceccarelli et al. 2020). Also, because these other taxa attach themselves to the substrate, they are not at risk of being deposited to the reef benthos by physical processes other than during periods of intense storms and wave action (Harmelin-Vivien 1994, Latypov 2007).

Porites superfusa is an encrusting coral that due to its morphology, can live in cryptic locations within the reef (Furby et al. 2017). Locations include cracks and crevices within rock substrate that other morphological types, such as massive morphology, cannot fit within. Therefore, encrusting colonies of *Porites superfusa* typically aggregate in areas of the reef with no heterospecifics, as displayed in imagery from sites at Palmyra Atoll (Fig. 10).

Fungia and *Porites superfusa* and their assigned morphologies are highly abundant within our analysis (Fig. 4 & 5). Due to this and their distinctive distributions within the reef environment, *Fungia*/solitary and *Porites superfusa*/encrusting colonies have several negative interspecific co-occurrences with other taxa and morphologies within our analyses (Tables 1 & 2).

4.5 Algae

In the taxa analysis, *Halimeda* has several positive co-occurrences with soft corals *Sinularia*, *Pachyclavularia*, and *Sarcophyton* (Table 1). In the morphology analysis,

morphological type algae has a positive co-occurrence with morphological type soft (Table 2). Soft corals create “halos of toxins” to prevent the colonization of their neighboring space by heterospecific corals, as discussed earlier. Therefore, the utilization of allelopathy provides ample colonization space for algae and other epizoic organisms to settle on the basal region of the stalk of the soft corals (Kerr & Paul 1995). Previous work has found that the arborescent shape of soft coral *Sinularia* provided refuge for *Halimeda* recruits as fish do not graze that close to the soft coral base (Kerr & Paul 1995). Kerr & Paul (1995) specifically found that algal biomass was significantly greater within 10 cm of *Sinularia* colonies compared to 10-30 cm away, supporting the analysis findings within this study. Also, during anti-predation situations, soft corals utilize aggressive behavior to damage neighboring scleractinian colonies. Soft corals can remove tissue from the skeleton of scleractinian corals, providing colonization space for algae. Therefore, soft coral aggression provides colonization space for algae around soft coral bases and on neighboring scleractinians, as seen in imagery from Palmyra Atoll (Fig. 11), leading to the positive interspecific co-occurrences between algae and soft coral found in this study (Tables 1 & 2).

Scleractinian coral and benthic algae interact with one another due to their shared need for resources such as sunlight and benthic space for survival (Benayahu & Loya 1981, McCook et al. 2001, Barott et al. 2012). Benthic algae utilize competitive behaviors such as overgrowth, shading, abrasion, and allelochemicals on scleractinian corals (McCook et al. 2001, Lirman 2001, Smith et al. 2006, Vermeij et al. 2009). These behaviors can prevent coral larvae settlement, and decrease coral growth and fecundity (River & Edmunds 2001, Titlyanov et al. 2007, Birrell et al. 2008, Chadwick & Morrow 2011). Benthic algae can cause coral death by enhancing microbial activity, which raises coral stress and disease (Smith et al. 2006, Vermeij et

al. 2009). Benthic algae can also serve as reservoirs of coral diseases, which leads to disease transmission when the two are in direct contact (Barott et al. 2009). Scleractinian coral can inhibit algal growth or kill benthic algae via overgrowth (McCook et al. 2001, McCook 2001). This intense algal-coral competition has led to zero positive co-occurrences between algae and scleractinian coral taxa within our taxa analysis (Table 1).

Differing morphological types of scleractinian corals have different encounters with benthic algae. Fast-growing corals such as branching morphologies are more likely to put energy into growth and less towards competition. This “escape in height” strategy means these morphological types can lower their exposure and competition with nearby benthic organisms such as algae (Meesters et al. 1996, Swierts & Vermeij 2016). Slower-growing scleractinian corals such as encrusting and massive morphologies are less likely to escape interactions with neighboring algae, therefore allocate more energy to competition than faster-growing corals (Swierts & Vermeij 2016). Colony size also impacts algae-coral interactions, with larger-bodied colonies less likely affected by overgrowth or shading by benthic algae (McCook et al. 2001, Barott et al. 2012). In our morphology analysis, algae has interspecific positive co-occurrences with morphologies massive and submassive (Table 2). This result is due to these morphologies inability to outgrow algal neighbors. Although encrusting colonies are also unable to outgrow algal neighbors, morphology encrusting was not found in an interspecific positive co-occurrence with algae in our results. This is because encrusting taxa *Porites superfusa* makes up a majority (66.1%) of the total encrusting colonies in our analysis, and the taxon has demonstrated a cryptic distribution at Palmyra Atoll (Fig. 10).

The only negative co-occurrences found to be intraspecific in the taxa and morphology analysis involved macroalga *Halimeda* (Table 1) and morphological group algae (Table 2).

Halimeda is a calcifying macroalga that contributes significant amounts of calcareous sediment to the reef environment due to its high-speed growth rate (Drew 1983, Wizemann et al. 2014). The build-up of *Halimeda* sediment further reduces local currents, enhancing the accumulation of other material into these piles. Due to this, *Halimeda* has led to extensive bioherm (rock build-up via sedentary organisms) formations worldwide (Rees et al. 2006, Marshall & Davies 1988).

Self-organization is the formation of patterns in the natural environment via biological or physical properties. Self-organization has been observed in the marine environment in intertidal oysters & mussels (Yurek et al. 2021, Liu et al. 2012). These specific spatial patterns via self-organization are displayed in some of the sites analyzed in this study (Fig. 12). It has been speculated that bioherms produced by *Halimeda* frequently have specific geomorphological patterns due to the biotic self-organization of this macroalga (McNeil et al. 2016).

The spatial orientation of *Halimeda* in some sites within our analysis created a distinct honeycomb pattern, leading to large gaps in *Halimeda* colonization from some sections of the substrate (Fig. 12a, b, c, d). Also, due to this spatial patterning, *Halimeda* patches are typically found in line formations with few patches of the macroalga neighboring one another (Fig. 12e). When not in line formations via self-organization, *Halimeda* is typically found neighboring soft corals in massive singular clumps, with few intraspecific neighboring occurring (Fig. 11). Therefore, the colonization patterns of the macroalga has resulted in the negative intraspecific co-occurrence of *Halimeda* in the taxa analysis (Table 1). *Halimeda* makes up 94% of the total algae count over all 14 sites, which explains the negative intraspecific co-occurrence of algae in the morphology analysis (Table 2).

Dictyosphaeria is the only alga part of an intraspecific positive co-occurrence in the taxa analysis (Table 1). *Dictyosphaeria* is a green macroalga that commonly settles on live coral or reef rock outcrops (Stimson et al. 2001, Stimson & Conklin 2008). It can also settle on large patches of sediment that previously hampered coral growth. Due to its ability to colonize substrate that other taxa cannot, *Dictyosphaeria* is in a positive intraspecific co-occurrence in this study (Table 1).

4.6 Successional Levels

All sites with nonlinear spatial determinism and thus in intermediate levels of succession were located on the north side of the Atoll (Fig. 8). Sites of spatial randomness and thus in early or late levels of succession were located primarily on the south side of the Atoll (Fig. 8). Only sites in intermediate succession are highly dominated by soft corals *Sinularia*, *Sarcophyton*, *Pachycaulvularia*, and *Zooanthid*, and macroalga *Halimeda*.

Soft corals and *Halimeda* are fast colonizers, especially after disturbance events such as nutrient overload or sediment deposition (Benayahu & Loya 1977, Fleury et al. 2000, Peterson et al. 2002, Rabelo et al. 2013). Soft coral is especially known to overgrow other benthic organisms well (Griffith 1997). However, in the long term, *Halimeda* and these soft coral taxa are not dominant on the reef for long periods as they are both soft in material and thus vulnerable to their environment. Therefore, it is understandable that there is low coverage of these five taxa in sites that were recently disturbed (early succession stage) or exposed to physical events for extended periods (late succession stage).

Soft coral and *Halimeda* can occupy large extents of the reef environment. In Palmyra Atoll imagery, *Sinularia* colonies reached diameters upwards of 3 m, and *Halimeda* formed

extensive line formations across multiple sites. Therefore, only smaller patches of reef space are available for other coral and algae taxa to colonize in sites with a high presence of soft coral and *Halimeda*. This increases the clustering and neighboring of these other colonies, thus decreasing random spatial patterning.

Also, we discovered that soft coral and *Halimeda* are in several positive interspecific co-occurrences in the taxa and morphology analyses (Tables 1 and 2). Consequently, in sites with higher coverage of these taxa, we can assume more interspecific neighboring is occurring. All 7 sites of intermediate succession had positive interspecific co-occurrences of *Sinularia* neighboring *Halimeda*, and *Halimeda* neighboring *Sinularia*. Also, 4 of the 7 intermediate sites had positive interspecific co-occurrences of *Sarcophyton* neighboring *Halimeda*. Therefore, a more substantial presence of soft coral and *Halimeda* in a site decreases random patterning and increases spatial predictability. This explains why sites of intermediate succession are more spatially deterministic than those of early or late succession.

CONCLUSION

3.1 Summary

The purpose of this study was to understand the neighborhood patterns of the scleractinian corals, soft corals, and algae present at the Palmyra Atoll reef ecosystem. Specifically, we wanted to understand neighborhood co-occurrence patterns that emerged from taxa and morphological pairings across all 14 sites from 2013.

Past methodologies relied upon to understand coral spatial patterns had several issues addressed with the updated methodology used within this study. Our utilization of large-area

imagery allowed us to examine neighborhood coral and algal patterns without manipulating their placement within the coral reef environment and perform analyses at a much larger scale than considered previously in the literature. Furthermore, our methodology utilizes incredibly high-detailed imagery that allows for the distinct borders of colonies to be drawn, recognition of colony-to-colony distinctions, and competency in including live coral and excluding dead coral mass from our data collection. This guarantees our ability to capture natural spatial patterns of scleractinian corals, soft corals, and algae at Palmyra Atoll.

In our analyses, we utilized a more complex buffer-based measurement that is more likely to find significant patterns than spatial point patterns. We also avoided using colonies' centroids and instead utilized their distinct boundary shapes to determine neighbor composition. Overall, this leads to a more comprehensive understanding of the co-occurrence patterns of coral and algae at Palmyra Atoll.

Via our methodology, we found few significant co-occurrence patterns in our results. This is due to our sites' high abundance of a few taxa and morphological types, and competition between colonies. From those significant patterns found, most positive co-occurrences were intraspecific and negative patterns interspecific. This is due to high interspecific competition and less intraspecific competition. Processes such as fragmentation and partial mortality lead to aggregations of conspecifics, influencing the majority of positive co-occurrences to be intraspecific within our results. Taxa such as *Fungia* and *Porites superfusa* reside in specific reef areas where heterospecifics do not. Due to this, both highly abundant taxa and their subsequent morphological groups are in multiple negative co-occurrences with others. Algae was in several interesting co-occurrence patterns, with macroalga *Halimeda* in intraspecific positive co-occurrences with soft corals; however, in a negative co-occurrence with itself due to biotic self-

organization. We also examined how spatial patterning between sites partially differed due to succession. Those sites on the south side of the atoll were in early or late succession, while those predominately on the north were in intermediate succession with high soft coral and *Halimeda* coverage. Presence of these taxa decreases random patterning and increases spatial predictability.

Our study has expanded our knowledge of coral spatial patterns while supporting the results of the few previous studies that analyzed the neighborhood patterns of coral colonies. We have therefore expanded upon a topic that previously there was little information on and also documented the co-occurrence patterns of algae, which had previously never been studied.

3.2 Improvements

There are specific methodological issues to be addressed to improve this study. Although utilizing large-area imagery dramatically improves our ability to analyze the reef environment on a large scale, stitching thousands of images to create one large photomosaic leads to distortions in the data. These include deformations in colony shapes and sizes, and the doubling or erasure of colonies within a final photomosaic. Given that our methodology relies heavily on the distinct borders of colonies and exact buffer measurements to analyze the neighborhood compositions, these distortions could impact our results. In this study, we also relied on a top-down view of the reef environment when tracing. The reef environment is not flat in topography; therefore, this top-down view cannot document all colonies that live within our site boundaries, including those growing below others or those in crevices in the substrate. Other methodological issues involve human error. Tracing is an intensive process that involves species identification of each colony found within a 100m² site. With such minute differences between some taxa, misidentification could occur. Tracing each colony outline by hand can also lead to errors in the borders, missing

lesions on the colony, and misinterpreting coral or algae as alive or dead matter. Eventually, utilizing AI-based software that draws colony borders and identifies taxa will decrease these human-based errors and make the tracing process more efficient.

3.3 Future Work

Previous neighbor pattern studies conducted on the Great Barrier Reef, Australia (Bradbury & Young 1983, Reichelt & Bradbury 1984) resulted in similar findings. However, given that all three studies including ours were conducted within the Pacific and this methodology is relatively untested, we cannot say that these results are universal. Therefore, expanding this methodology to other reef environments beyond the Pacific with similar and non-similar taxa/morphologies will bring insight into whether the neighborhood patterns we see in this study are reef-specific or ubiquitous.

Applying this methodology over multiple time points will bring insight into how changes in the physical reef environment, such as temperature fluctuations, storms, bleaching events, and other disturbance patterns, will impact neighbor patterns. Large-scale environmental disturbances can alter the physical structure of the reef via complete coral mass loss. We suspect that alterations to the reef environment of this magnitude would severely impact habitat-driven negative co-occurrences.

Material from this thesis is currently being prepared for submission for publication. Who's next door? Using GIS to understand neighbor patterns of coral and algae at Palmyra Atoll. McTague, Sarah; McNamara, Dylan; Edwards, Clinton; Pedersen, Nicole; Sandin, Stuart. The thesis author was the primary author of this material.

FIGURES



Figure 1: Satellite imagery of Palmyra Atoll and site locations. Inset map displays the location of Palmyra Atoll within the Pacific Ocean.

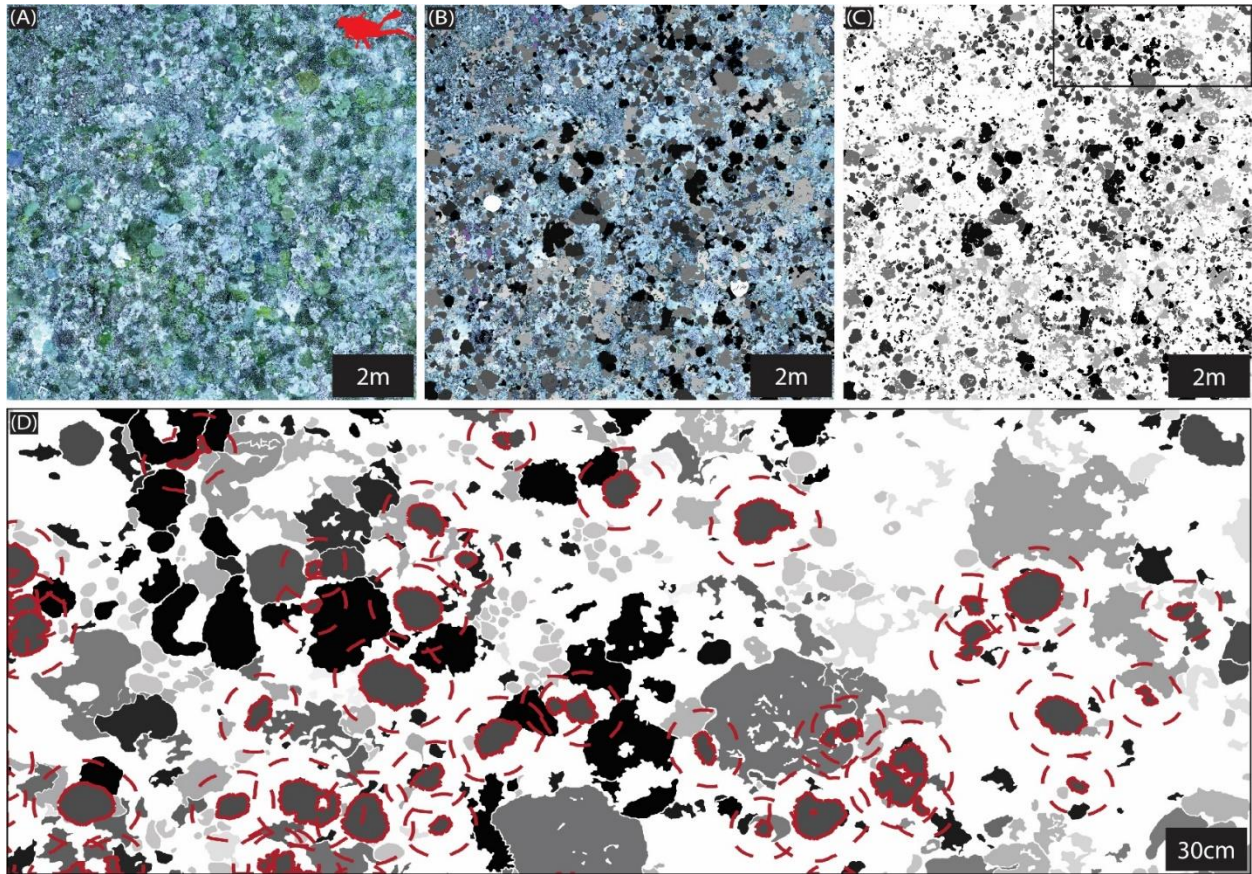


Figure 2: Process of 100 m² photomosaic plot. (a) Undigitized photomosaic plot with cartoon diver in the top right represents the size ratio between a human of average height (1.7 m) to a site at Palmyra Atoll. (b) Digitized photomosaic plot. Polygons are color-coded based on taxonomic classification. (c) Digitized plot converted into ArcGIS Pro as a vector layer file. Maintain polygon color to represent taxonomic classification. (d) Subsection of (c). Colonies of *Pocillopora* are depicted as gray polygons with red outlines. Buffers of *Pocillopora* that fall within the photomosaic boundary are depicted as red dashed lines, and those that fall outside have been cut as per the study's methodology. Buffers of all other taxonomic groups in this site are not depicted.

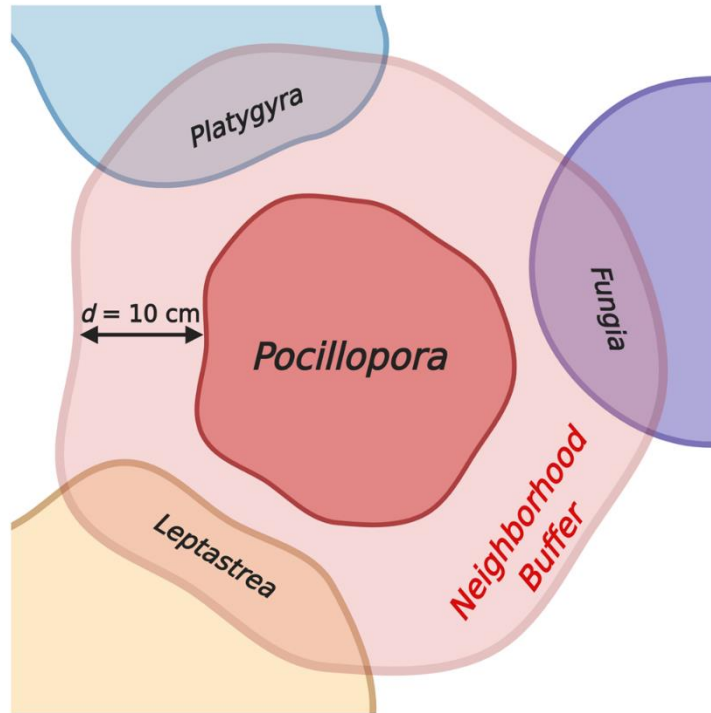


Figure 3: Cartoon depicting a neighborhood buffer with a distance $d=10$ cm of a colony of *Pocillopora*. The buffer generated only consists of the space of a distance d outside the *Pocillopora* polygon and excludes the colony itself. This example has a neighborhood composition of three coral taxa: *Platygyra*, *Fungia*, and *Leptastrea*.

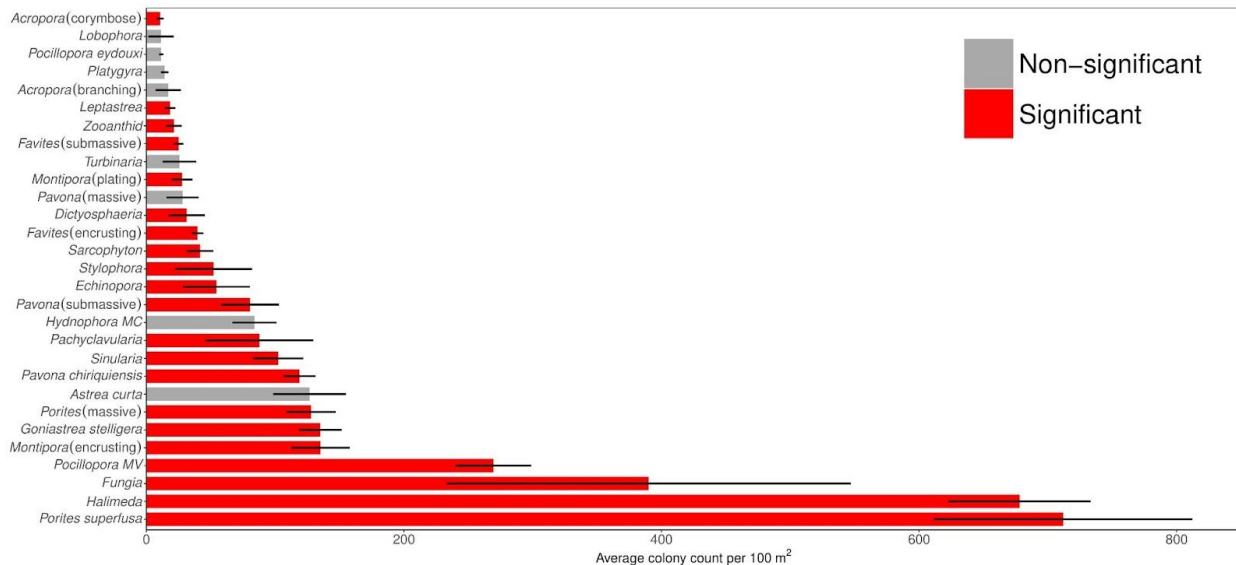


Figure 4: Mean abundance of colony taxa counts per 100 m² site. Error bars are +/- 1 standard error. Taxa depicted in red are involved in at least one significant co-occurrence, and taxa depicted in grey are not involved in any significant co-occurrences. Only the 29 most abundant taxa are shown out of the 52 total.

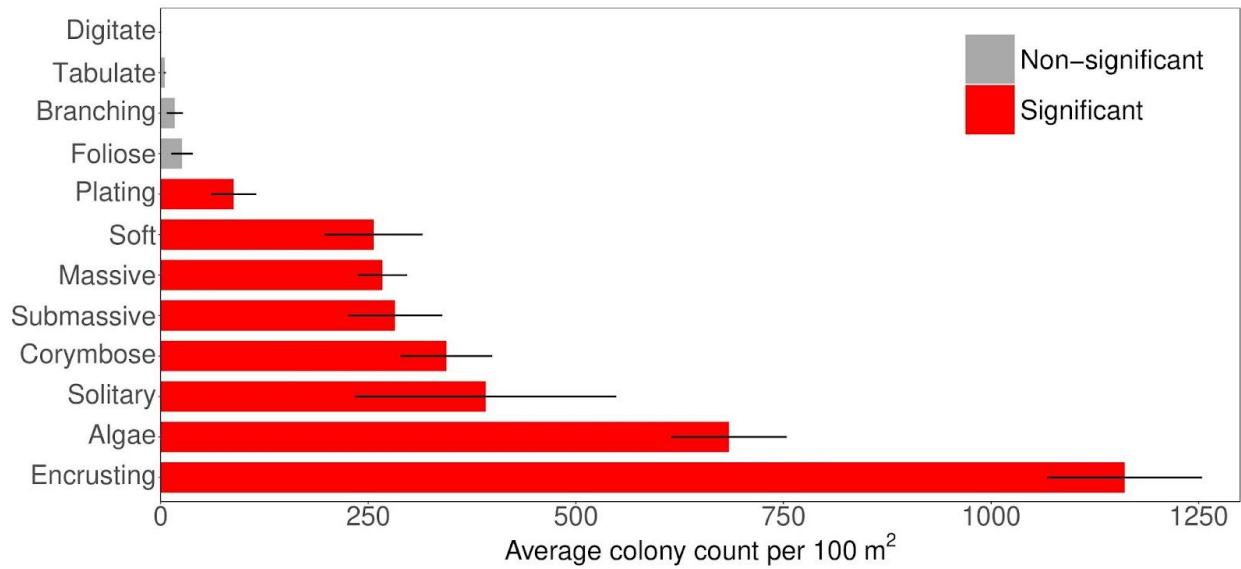


Figure 5: Mean abundance of colony morphology counts per 100 m² site. Error bars are +/- 1 standard error. Morphologies depicted in red are involved in at least one significant co-occurrence, and morphologies depicted in grey are not involved in any significant co-occurrences.

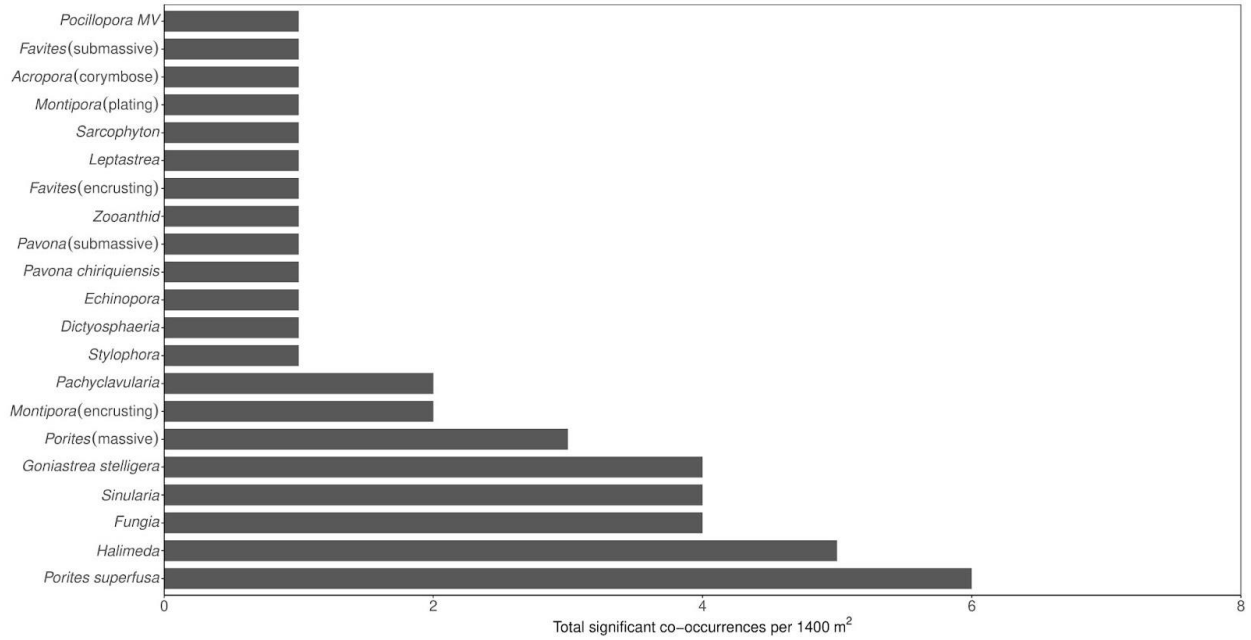


Figure 6. Total count of significant co-occurrences (positive and negative) for each taxon. Taxa part of only non-significant co-occurrences were not included.

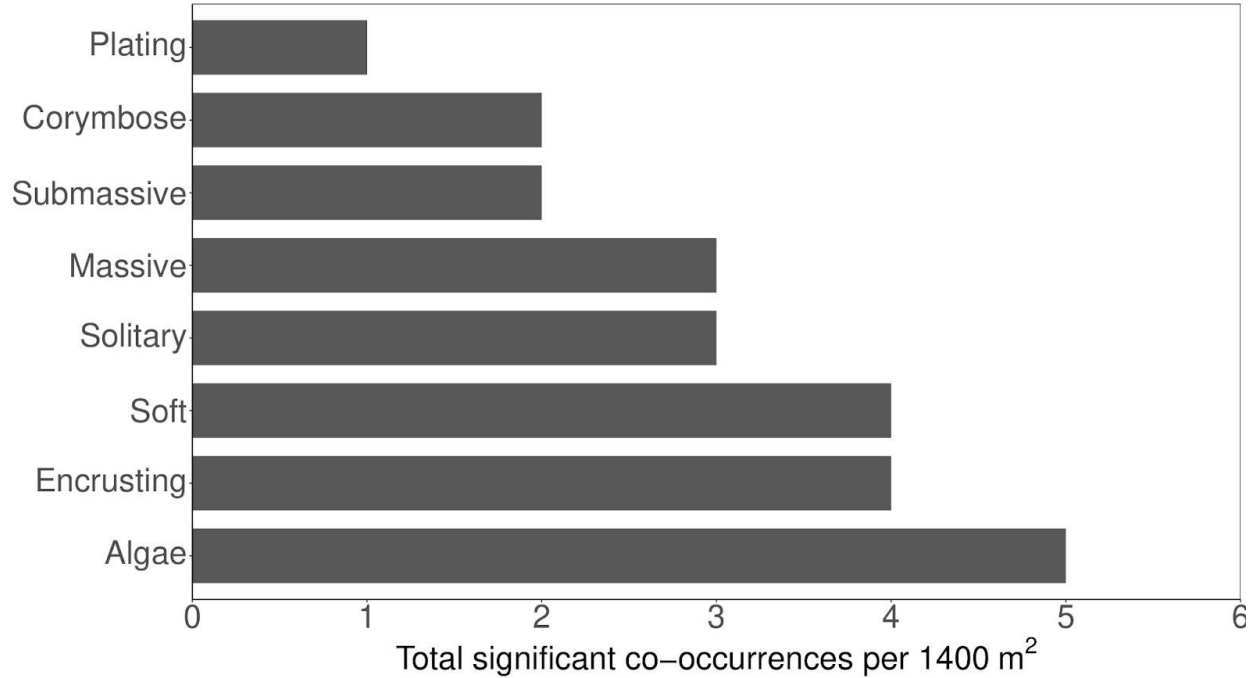


Figure 7. Total count of significant co-occurrences (positive and negative) for each morphological group. Morphologies part of only non-significant co-occurrences were not included.



Figure 8. Fig. 1 with sites color-coded by successional stage. Sites in green are in an early or late stage of succession, and sites in red are in an intermediate stage.

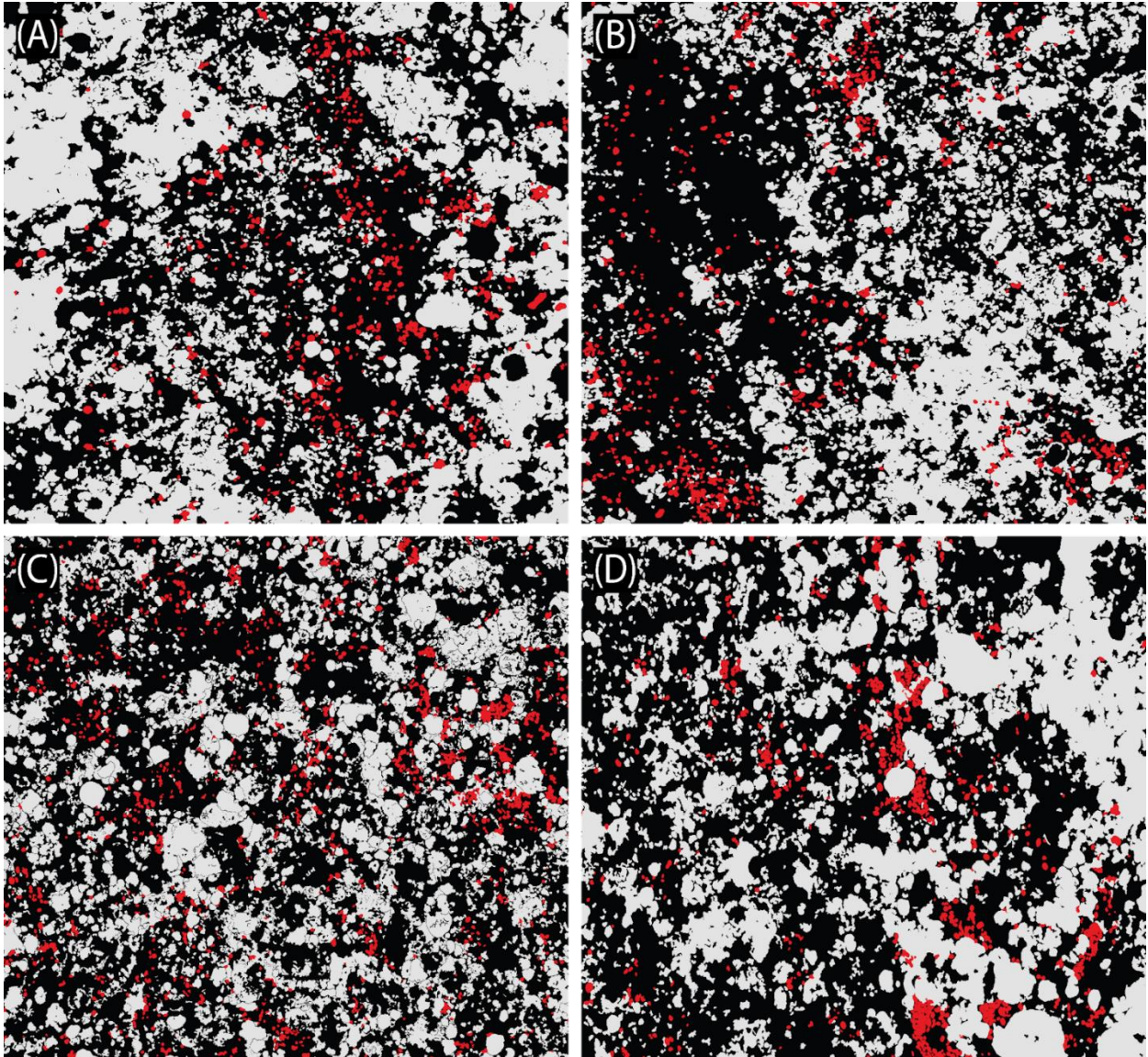


Figure 9. *Fungia* colonies at Palmyra Atoll. Annotations of *Fungia* in red against a black background to observe the aggregative behaviors of the solitary coral at 4 separate sites. All other taxa are displayed in gray. (a) Site FR3. (b) FR4. (c) FR9. (d) FR13.

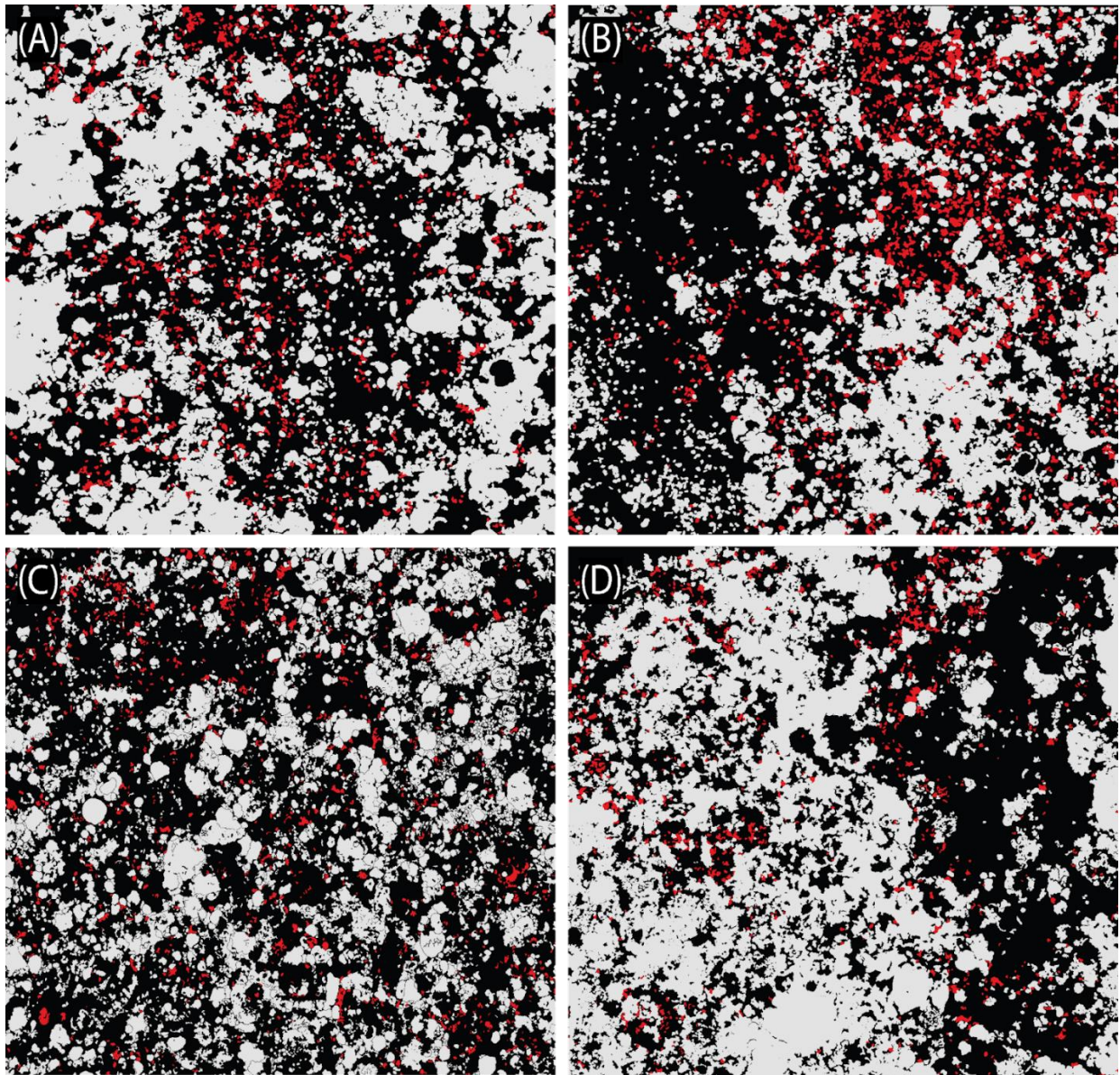


Figure 10. *Porites superfusa* colonies at Palmyra Atoll. Annotations of *Porites superfusa* in red against a black background to observe the aggregative behaviors of the encrusting coral at 4 separate sites. All other taxa are displayed in gray. (a) Site FR3. (b) FR4. (c) FR9. (d) FR69.

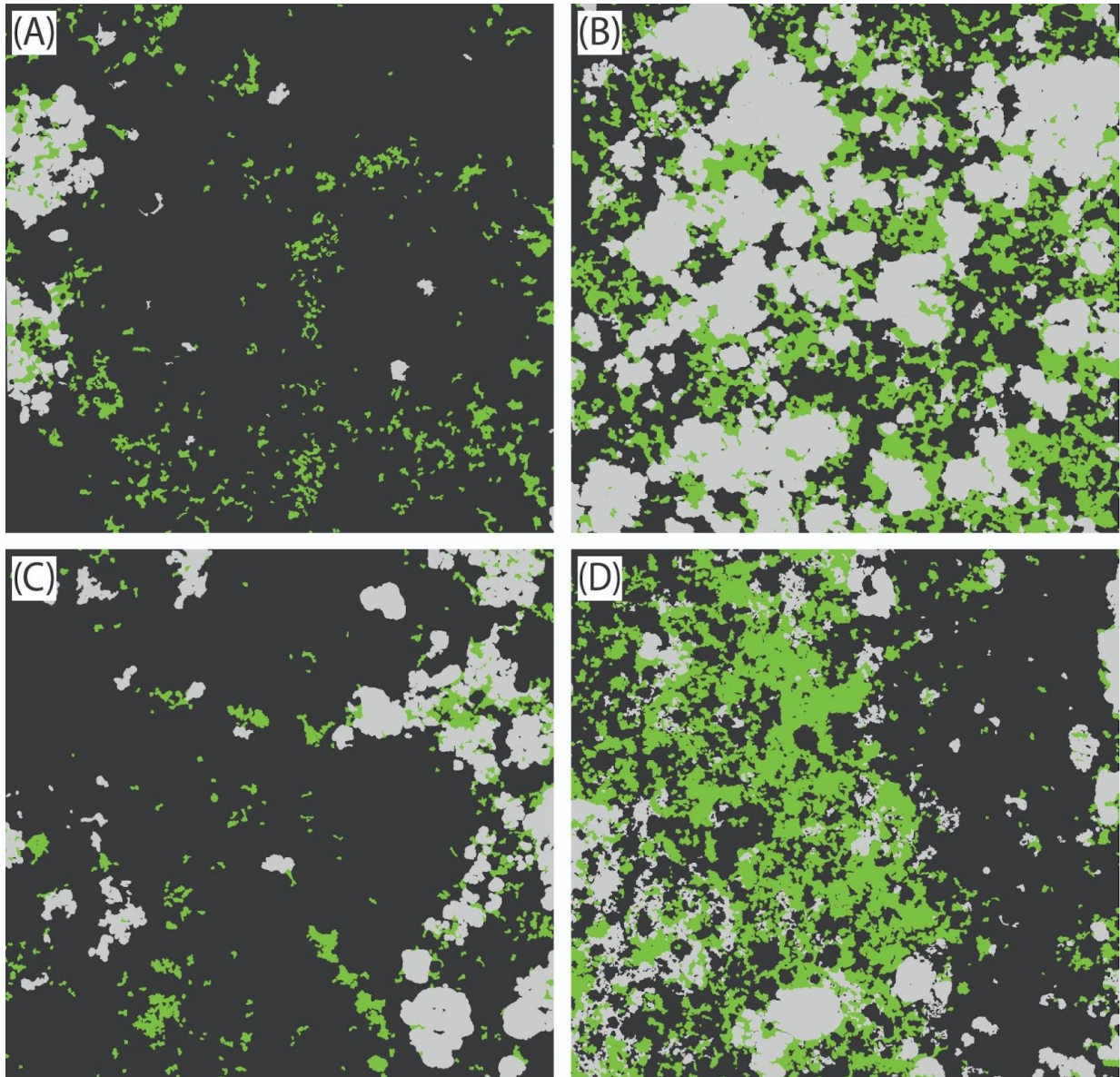


Figure 11. *Halimeda* and soft coral colonies at Palmyra Atoll. Annotations of *Halimeda* in green and soft coral in grey against a black background at 4 separate sites. All other taxa are not displayed. (a) Site FR3. (b) FR7. (c) FR13. (d) FR69.

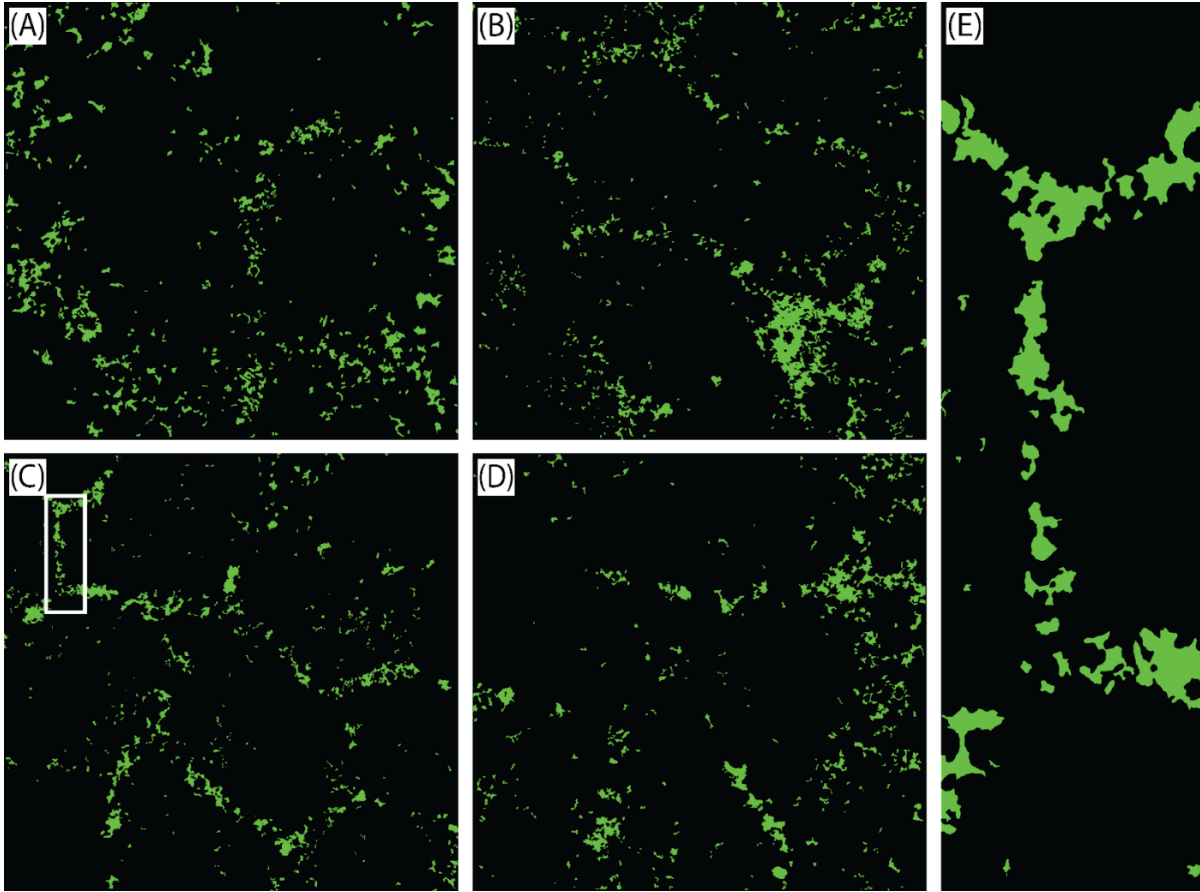


Figure 12. *Halimeda* patches at Palmyra Atoll. Annotations of *Halimeda* in green against a black background to observe the alga's distinct polygonal spatial patterns at 4 separate sites. (a) Site FR3. (b) FR4. (c) FR9. (d) FR13. (e) Subsection of (c).

TABLES

Table 1: Descriptions of statistically significant patterns of co-occurrence between taxa pairs. Final positive co-occurrences between pairings are above double line and negative co-occurrences are below. Further displayed are the number of sites where positive co-occurrence, negative co-occurrence and non-significant co-occurrence occur between each taxa pairing. The order of taxa pairing are from strongest co-occurrence on top to lowest on bottom. This applies to both the top and bottom sections of table.

Buffer taxon	Neighbor taxon	Number of Sites		
		Positive	Negative	Non-sig
<i>Stylophora</i>	<i>Stylophora</i>	5	0	0
<i>Porites superfusa</i>	<i>Porites superfusa</i>	13	0	1
<i>Montipora</i> (encrusting)	<i>Montipora</i> (encrusting)	13	0	1
<i>Fungia</i>	<i>Fungia</i>	13	0	1
<i>Halimeda</i>	<i>Sinularia</i>	12	0	1
<i>Dictyosphaeria</i>	<i>Dictyosphaeria</i>	7	0	1
<i>Pachyclavularia</i>	<i>Pachyclavularia</i>	7	0	1
<i>Echinopora</i>	<i>Echinopora</i>	6	0	1
<i>Pavona chiriquiensis</i>	<i>Pavona chiriquiensis</i>	12	0	2
<i>Pachyclavularia</i>	<i>Halimeda</i>	6	0	2
<i>Sinularia</i>	<i>Halimeda</i>	10	0	4
<i>Pavona</i> (submassive)	<i>Pavona</i> (submassive)	8	0	4
<i>Zooanthid</i>	<i>Zooanthid</i>	8	0	4
<i>Goniastrea stelligera</i>	<i>Goniastrea stelligera</i>	9	0	5
<i>Favites</i> (encrusting)	<i>Favites</i> (encrusting)	9	0	5
<i>Leptastrea</i>	<i>Leptastrea</i>	8	0	5
<i>Sarcophyton</i>	<i>Halimeda</i>	6	0	4
<i>Montipora</i> (plating)	<i>Montipora</i> (plating)	7	0	5
<i>Acropora</i> (corymbose)	<i>Acropora</i> (corymbose)	7	0	5
<i>Porites</i> (massive)	<i>Porites</i> (massive)	7	0	6
<i>Favites</i> (submassive)	<i>Favites</i> (submassive)	7	0	6
<i>Porites superfusa</i>	<i>Sinularia</i>	0	12	1
<i>Porites superfusa</i>	<i>Montipora</i> (encrusting)	0	11	3
<i>Porites superfusa</i>	<i>Porites</i> (massive)	1	10	2
<i>Fungia</i>	<i>Sinularia</i>	0	9	4
<i>Fungia</i>	<i>Pocillopora</i>	0	8	6
<i>Halimeda</i>	<i>Halimeda</i>	1	9	4
<i>Porites superfusa</i>	<i>Goniastrea stelligera</i>	0	8	6
<i>Fungia</i>	<i>Goniastrea stelligera</i>	0	8	6
<i>Porites</i> (massive)	<i>Porites superfusa</i>	0	7	6

Table 2: Descriptions of statistically significant patterns of co-occurrence between morphological pairs. Final positive co-occurrences between pairings are above double line and negative co-occurrences are below. Further displayed are the number of sites where positive co-occurrence, negative co-occurrence and non-significant co-occurrence occur between each morphological pairing. The order of taxa pairing are from strongest co-occurrence on top to lowest on bottom. This applies to both the top and bottom sections of table.

Buffer Morphology	Neighbor Morphology	Number of Sites		
		Positive	Negative	Non-sig
Solitary	Solitary	13	0	1
Soft	Algae	12	0	2
Plating	Plating	12	0	2
Encrusting	Encrusting	12	0	2
Algae	Soft	12	0	2
Submassive	Submassive	11	0	3
Massive	Massive	10	0	4
Massive	Algae	9	0	1
Algae	Submassive	8	0	6
Encrusting	Soft	0	12	2
Encrusting	Massive	0	10	4
Algae	Algae	1	10	3
Solitary	Corymbose	0	9	5
Corymbose	Soft	0	9	5
Solitary	Encrusting	0	10	4

SUPPLEMENTAL

Table S 1: List of each morphological type included in study and colony count of each morphology over all sites. Further included is every taxon found within each morphological type and taxon colony count. Example photographs of each morphological type taken directly from photomosaics of Palmyra Atoll that were used in the analysis of this study. Bolded taxon name under each morphological type correlates with type of taxon depicted in example morphology photograph.

Hard coral morphological types		
Morphological Type	Species within Morphology	Example
Branching (n=239)	<i>Acropora</i> sp. (branching) (n=239)	
Corymbose (n=4817)	<i>Acropora</i> sp. (corymbose) (n=150), <i>Pocillopora damicornis</i> (n=1), <i>Pocillopora eydouxi</i> (n=161), <i>Pocillopora</i> sp. (n=3774), <i>Stylophora pistillata</i> (n=731)	
Digitate (n=6)	<i>Acropora</i> sp. (digitate) (n=6)	
Encrusting (n=15073)	<i>Astrea curta</i> (n=1776), <i>Favites</i> sp. (encrusting) (n=558), <i>Favites russeli</i> (n=1), <i>Leptastrea</i> sp. (n=259), <i>Leptastrea purpurea</i> (n=1), <i>Leptoseris</i> sp. (n=43), <i>Montipora capitata</i> (n=1), <i>Montipora</i> sp. (encrusting) (n=1893), <i>Pavona chiriquiensis</i> (n=1665), <i>Pavona varians</i> (n=4), <i>Porites superfusa</i> (n=8787) , <i>Psammocora</i> sp. (n=80), <i>Psammocora profundacella</i> (n=5)	
Foliose (n=361)	<i>Turbinaria reniformis</i> (n=361)	
Massive (n=3738)	<i>Astropora</i> sp. (n=5), <i>Dipsastrea matthai</i> (n=20), <i>Hydnophora microconos</i> (n=1176), <i>Lobophyllia</i> sp. (n=71), <i>Pavona</i> sp. (massive) (n=395), <i>Platyggyra</i> sp. (n=200) , <i>Porites lobata</i> (n=74), <i>Porites</i> sp. (massive) (n=1791), <i>Porites rus</i> (n=6)	
Plating (n=1231)	<i>Echinopora</i> sp. (n=763), <i>Hydnophora exesa</i> (n=71), <i>Montipora FC</i> (n=8), <i>Montipora</i> sp. (plating) (n=389)	
Solitary (n=5481)	<i>Fungia</i> sp. (n=5460) , <i>Halomitra</i> sp. (n=21)	
Submassive (n=3436)	<i>Astrea annuligera</i> (n=14), <i>Favites</i> sp. (submassive) (n=353), <i>Gardineroseris</i> sp. (n=43), <i>Goniastrea pectinata</i> (n=7), <i>Goniastrea stelligera</i> (n=1891) , <i>Pavona</i> sp. (submassive) (n=1128)	
Tabulate (n=69)	<i>Acropora</i> sp. (tabulate) (n=69)	

Other morphological types

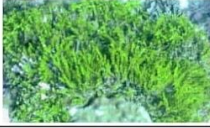
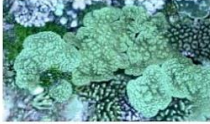
Morphological Type	Species within Morphology	Example
Algae (n=10097)	<i>Caulerpa</i> sp. (n=4), <i>Dictyosphaeria</i> spp. (n=440), <i>Halimeda</i> spp. (n=9493) , <i>Lobophora variegata</i> (n=160)	
Soft coral (n=3590)	<i>Pachyclavularia</i> sp. (n=1229), <i>Corallimorph</i> sp. (n=41), <i>Sarcophyton</i> sp. (n=585), <i>Sinularia</i> sp. (n=1434) , <i>Zooanthid</i> sp. (n=301)	

Table S 2: Descriptions of statistically significant patterns of co-occurrence between taxa pairs from analysis lacking algae and *Fungia* colonies. Final positive co-occurrences between pairings are above double line and negative co-occurrences are below. Further displayed are the number of sites where positive co-occurrence negative co-occurrence and non-significant co-occurrence occur between each taxa pairing. The order of taxa pairing are from strongest co-occurrence on top to lowest on bottom. This applies to both the top and bottom sections of table.

Buffer taxon	Neighbor taxon	Number of Sites		
		Positive	Negative	Non-sig
<i>Montipora</i> (encrusting)	<i>Montipora</i> (encrusting)	14	0	0
<i>Porites superfusa</i>	<i>Porites superfusa</i>	13	0	1
<i>Pachyclavularia</i>	<i>Pachyclavularia</i>	7	0	1
<i>Pavona chiriquiensis</i>	<i>Pavona chiriquiensis</i>	12	0	2
<i>Goniastrea stelligera</i>	<i>Goniastrea stelligera</i>	11	0	3
<i>Astrea curta</i>	<i>Astrea curta</i>	6	0	2
<i>Hydnophora microconos</i>	<i>Hydnophora microconos</i>	9	0	3
<i>Pavona</i> (submassive)	<i>Pavona</i> (submassive)	9	0	3
<i>Leptastrea</i>	<i>Leptastrea</i>	8	0	5
<i>Porites</i> (massive)	<i>Porites</i> (massive)	8	0	5
<i>Montipora</i> (plating)	<i>Montipora</i> (plating)	7	0	5
<i>Zooanthid</i>	<i>Zooanthid</i>	7	0	5
<i>Favites</i> (encrusting)	<i>Favites</i> (encrusting)	8	0	6
<i>Sinularia</i>	<i>Sinularia</i>	8	0	6
<i>Acropora</i> (corymbose)	<i>Acropora</i> (corymbose)	7	0	6
<i>Favites</i> (submassive)	<i>Favites</i> (submassive)	7	0	6
<i>Porites superfusa</i>	<i>Montipora</i> (encrusting)	0	12	2
<i>Montipora</i> (encrusting)	<i>Porites superfusa</i>	0	10	4
<i>Porites superfusa</i>	<i>Sinularia</i>	0	9	5
<i>Porites</i> (massive)	<i>Porites superfusa</i>	0	8	5
<i>Porites superfusa</i>	<i>Porites</i> (massive)	1	9	3
<i>Porites superfusa</i>	<i>Goniastrea stelligera</i>	0	8	6
<i>Sinularia</i>	<i>Porites superfusa</i>	0	7	7

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