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Thesis of
Daniel Perez

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

April 2023

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Thesis Committee

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NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

Twenty Years of Change in a Southeast Florida *Acropora cervicornis* Thicket

Daniel M. Perez

Submitted to the Faculty of Halmos College of Arts and Sciences in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:
Marine Science
Nova Southeastern University
April 2023

Abstract

Acropora cervicornis is a species of stony coral that can exist in large thickets that provide functionally unique habitat. However, populations have declined by 98% in some areas of the Caribbean. Even in death, the structure from an *A. cervicornis* thicket provides surface area for the attachment of benthic organisms. Broward County *Acropora* (BCA) is an *A. cervicornis* thicket, located off Fort Lauderdale, Florida, which has been monitored since 2003. The objective of this study was to describe the temporal changes in community structure in response to 20 years of disturbances affecting BCA. Data was collected by taking images along four linear transects to assess temporal changes in percent benthic cover from 2003-2022. *Acropora cervicornis* cover declined from 34.8 ± 2% in 2003 to 2.4 ± 0.6% in 2022. The most severe declines observed were related to thermal stress, tropical storm and hurricane damage, disease, and predation in 2005-2006, 2010-2011, and 2015-2016. As *A. cervicornis* died, other taxa utilized the remaining dead structure, with increases in *Agaricia agaricites*, macroalgae, and crustose coralline algae cover observed. There was also evidence of structural decline toward the end of the study. Based on the detected trends, it is likely this long-term monitoring effort will capture the complete loss of this unique and complex habitat in the coming years. Thicket recovery will likely require active restoration and a reduction in local stressors. These remnant thickets are valuable research areas, as they provide opportunities to assess community dynamics, resilience, succession, and the response to disturbances.

Keywords: Benthic community, Long-term coral reef monitoring, Coral reef disturbance, Tropical storms, Hurricanes, Temperature stress

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Introduction

The Atlantic staghorn coral, *Acropora cervicornis*, has experienced severe declines within the last several decades (Aronson & Precht, 200l; Goergen *et al*., 2020) and is currently listed as 'threatened' under the US Endangered Species Act and 'critically endangered' on the International Union for Conservation of Nature (IUCN) Red List (Hogarth, 2006). Once dominant along forereefs throughout the Caribbean, populations have experienced declines of 80-90% with some areas experiencing losses of up to 98% (Aronson & Precht, 200l; Bruckner, 2002; Miller *et al*., 2002). These declines are due to a variety of disturbances and stressors including disease (Davis, 1982; Aronson & Precht, 200l; Miller *et al*., 2002; Bruno *et al*., 2007; Lirman *et al*., 2010; Brandt *et al*., 2013; Goergen *et al*., 2019; Goergen *et al*., 2020;), predation (Knowlton *et al*., 1990; Lirman *et al*., 2010; Goergen *et al*., 2019; Goergen *et al*., 2020), thermal stress (Bruno *et al*., 2007; Lirman *et al*., 2010; Lirman *et al*., 2011; Jones *et al*., 2020), and tropical storms and hurricanes (Knowlton *et al*., 1990; Miller *et al*., 2002; Gardner *et al*., 2005; Brandt *et al*., 2013; Goergen *et al*., 2019; Goergen *et al*., 2020). Many of these disturbances can interact, causing further declines (Knowlton *et al*., 1990; Wilkinson & Souter, 2008; Goergen *et al*., 2019; Goergen *et al*., 2020; Renzi *et al*., 2022). As a result, there are very few areas where the species is thriving today (Greer *et al*., 2020). According to the fossil record, *A. cervicornis* has historically survived through many disturbances and thus the recent declines can be considered unusual (Greer *et al*., 2009).

Acropora cervicornis has a fast growth rate and prolific branching morphology and can reproduce through asexual fragmentation; these characteristics allow *A. cervicornis* to propagate quickly (Tunnicliffe, 1981; Neigel & Avise, 1983; Vargas-Angel *et al*., 2006) and form large patches or thickets (Lirman *et al*., 2010; Larson *et al*., 2014; Huntington *et al*., 2017; Walker, 2017). Much like general *A. cervicornis* population trends, the abundance, distribution, and extent of these thickets has declined and although rare, large and dense thickets still exist (Vargas-Angel *et al*., 2003; Lirman *et al*., 2010; Walker, 2017). The complexity and habitat framework created by *A. cervicornis* thickets are unique and serve a critical and irreplaceable ecological role in Caribbean coral reef ecosystems (Goergen *et al*., 2019). These thickets provide important habitat for a variety of reef fish and other organisms as well as being a significant contributor to reef accretion (Precht *et al*., 2002). *Acropora cervicornis* growth maintains thicket functions and their dead skeletons also provide substrate for coral settlement (Bozec *et al*., 2015), as well as other benthic groups (Greenstein *et al*., 1998; Aronson & Precht, 2001; Caterham *et al*., 2019; Jones & Gilliam, 2020; Gilliam *et al.*, 2021). Macroalgae, zoanthids, tunicates, and sponges have been documented to colonize dead *Acropora* framework (Norström *et al*., 2009; Tkachenko *et al.*, 2007; Caterham *et al.*, 2019) and may contribute significantly to benthic cover over time (Hughes *et al.*, 2010). The abundance of "weedier" stony coral species, such as *Porites astreoides* and *Agaricia* species, are documented to increase when other reef-building species decrease (Robbart *et al*., 2004; Green *et al.*, 2008; Kenkel *et al.*, 2013; Caterham *et al*., 2019; Lenz *et al*., 2021). These same stony coral species have been shown to settle and grow on dead *A. cervicornis* framework (Greenstein *et al.*, 1998; Aronson & Precht, 2001; Caterham *et al*., 2019; Jones & Gilliam, 2020; Gilliam *et al.*, 2021), and they may have greater resilience toward a changing ecosystem (Robbart *et al*., 2004; Alvarez-Filip *et al*., 2009a; Soto-Santiago *et al*., 2017; Caterham *et al*., 2019; Lenz *et al.*, 2021). Although, studies have documented the settlement and growth of benthic taxa on dead *A. cervicornis* structure, few studies have been conducted to document long-term changes in the benthic community structure as the dead *A. cervicornis* structure erodes through time if not replaced by live *A. cervicornis*.

Acropora cervicornis thickets have historically been found throughout Florida's Coral Reef (FCR), but more recently appear to be more common in the northern region of FCR, known as the Kristin Jacobs Coral Reef Ecosystem Conservation Area (Coral ECA) (Walker, 2017). *Acropora cervicornis* thickets in the Coral ECA represent the northernmost extent of this important habitat (Walker, 2017). Previous monitoring assessments within the Coral ECA have shown spatial and temporal variation in the size, overall health, and percent benthic cover of *A. cervicornis* thickets (Vargas-Angel *et al*., 2003; Walker *et al*., 2012; Walker, 2017; Goergen *et al.*, 2019), but these were one-time assessments or monitoring studies focused solely on *A. cervicornis*. With more frequent disturbances, such as thermal stress, tropical storms and hurricanes, disease, and predation, long-term monitoring is needed to assess temporal changes in *A. cervicornis* as well as the associated benthic community within thickets. These remnant thickets provide a glimpse of the former prevalence of *A. cervicornis* and are valuable research areas, as they provide opportunities to assess community dynamics, resilience, succession, and the response to disturbances.

Due to numerous disturbance events impacting these unique habitats, a comprehensive and long-term monitoring study is required to identify threats to the habitat, quantify benthic community change, and develop effective management strategies. The objective of this study was to describe changes in benthic community structure of an *A. cervicornis* thicket, Broward County *Acropora* (BCA), in response to 20 years of disturbances. My study addresses three questions 1) how the *Acropora cervicornis* population has changed over time at BCA, 2) what disturbance events may have contributed to these population changes, and 3) how have these changes impacted the benthic community structure. To address these questions, I analyzed annual percent benthic cover of living *A. cervicornis*, dead *A. cervicornis*, and other benthic community taxa and stony coral demographic data using long-term monitoring data collected over a period of 20 years along permanent transects established at BCA. These data were collected as part of the Southeast Coral Reef Evaluation and Monitoring Project (SECREMP) (Gilliam *et al*., 2021). A literature review of disturbance events that impacted the region around BCA were then related to changes in benthic cover for *A. cervicornis* and other benthic taxa. The results of this study represent two decades of dynamic changes in an *A. cervicornis* thicket in the Coral ECA, which can inform researchers and resource managers on how multiple disturbance events over long periods of time can inhibit recovery of the essential ecological services associated with *A. cervicornis* thickets throughout its range.

Methods

Study Site

BCA is an *A. cervicornis* thicket located offshore Broward County, Florida in the Coral ECA near the northernmost extent of the species range. With an area greater than 10,425 m^2, BCA lies 380 m from shore along the nearshore ridge complex in 6 m of water (center coordinates: 26° 08.985’ N, 80° 05.810’ W) (Vargas-Angel *et al.*, 2003; Walker *et al*., 2012; Goergen *et al.*, 2019; Jones & Gilliam, 2020; Gilliam *et al*., 2021). It was first described by Vargas-Angel *et al*. (2003) and various aspects of its extent and condition have been documented in Walker *et al*. (2012), Goergen *et al*. (2019), and Jones & Gilliam (2020).

Data Collection

BCA is one of the long-term SECREMP monitoring sites offshore Broward County, Florida (Gilliam *et al*., 2021). Temporal changes in *A. cervicornis* population and community structure were analyzed annually at four permanent stations in BCA from 2003-2022. Stations were assessed in June of each year except for 2011 and 2020, when they were assessed in July. The site consisted of four 22 m long fixed, permanent stations with stakes marking each end. Each of the four stations consisted of three 22 m parallel linear transects separated by 1 m. Benthic transect images were collected along each of the three transects at each station. Linearly along each station transect approximately 60, 40 cm wide abutting images were taken at a fixed distance from the substrate. Each transect covered approximately 8.8 m² of substrate, with a station total area of 26.4 m² and a site total area of 105.6 m². For this study, images were analyzed using Point Count with Excel Extensions (CPCe) (Kohler & Gill, 2006). The benthic taxa directly under 15 randomly generated points on each image were identified, totaling approximately 900 points per transect. Benthic community taxa aside from *A. cervicornis* included other scleractinian (stony) corals to species, macroalgae, sponge, crustose coralline algae (CCA), encrusting and branching gorgonians, zoanthids, and other living biota (e.g., hydroids, anemones, etc.). Substrate categories included dead *A. cervicornis* (standing dead branches and rubble) and hardbottom substrate (any substrate that was not dead *A. cervicornis*). In this study, the benthic community taxa together with living *A. cervicornis*, dead *A. cervicornis*, and hardbottom will be referred to as the benthic community structure. Non-*A. cervicornis* stony corals were pooled together for some analyses into a group called “other coral” due to their low cover percentages as individual species. “Other living biota” were pooled together due to their low cover percentages as individual groups, and cyanobacteria were grouped with macroalgae due to identification challenges, especially from images taken in earlier years. During image analysis, points that landed on benthic community taxa growing on dead *A. cervicornis* substrate were differentiated from those growing on hardbottom.

Stony coral demographic data was collected within a 1 m x 22 m belt transect around the center transect within each station from 2012-2022. Stony coral demographic data was not included in the SECREMP sampling protocols prior to 2012 (Gilliam *et al*., 2021). Stony corals were identified to species, colony diameter was measured, and health conditions (presence of bleaching, disease, and/or predation) were recorded for all colonies ≥4 cm in diameter within 50 cm of either side of the transect. The sample area for each station was 22 m², for a site total of 88 m². Stony coral demographic data does not include *A. cervicornis* because individual colonies could not be identified in a thicket due to their interconnected, complex branching morphology.

Disturbances

Examination of published literature was conducted to identify disturbance events that may have impacted BCA during the study period (Table 1). In 2005, a warm water anomaly affected many parts of the Caribbean, causing mass stony coral mortality (Wilkinson & Souter, 2008; Eakin *et al*., 2010). In 2009, between May and mid-October, above-average air temperatures were recorded, resulting in sea surface temperatures (SST) above 30 °C for over 80 days (Goergen *et al*., 2019). In 2010, an unprecedented cold-water event occurred, causing significant coral mortality along the FCR (Lirman *et al*., 2011). In 2012, there was higher recorded disease incidence at BCA compared to other years (Goergen *et al*., 2019). In late 2014 through 2015, warm temperatures were recorded throughout the Coral ECA (Goergen *et al*., 2019; Jones *et al*., 2020). There was also significant predation (fireworm, *Hermodice carunculata*) and disease prevalence recorded at BCA in 2015 (Goergen *et al*., 2019).

Table 1. Disturbances identified as part of the literature review with their respective date ranges and references used for the study. Exact dates were used if they were available; if not, ranges or years were used.

Disturbance	Dates	Reference
Heat Stress	May-October 2005 May-November 2005	Wilkinson & Souter, 2008 Eakin *et al.,* 2010
Heat Stress	May-October 2009	Goergen *et al.,* 2019
Cold Stress	January-March 2010 2010	Lirman *et al.,* 2011 Jones *et al.*, 2020
Disease Event	September 10, 2012	Goergen *et al.,* 2019
Heat Stress	Summer 2014	Goergen *et al.,* 2019
Heat Stress	Summer 2015 2015	Goergen *et al.,* 2019 Jones *et al.,* 2020
Disease Event	Summer 2015	Goergen *et al.,* 2019
Predation Event	Summer 2015	Goergen *et al.,* 2019

Increased wave and surge energy associated with tropical storms and hurricanes may be significant drivers of stony coral mortality (Knowlton *et al*., 1990; Brandt *et al*., 2013). Tropical storm and hurricane wind data were gathered from individual reports detailed in the National Hurricane Center and Central Pacific Hurricane Center website managed by the National Oceanographic and Atmospheric Administration (NOAA) (nhc.noaa.gov) (Table 2). NOAA defines a tropical storm as a tropical cyclone where the maximum sustained surface wind speed, which is the highest one-minute average wind (measured at a height of 10 meters with unobstructed exposure) associated with the system at a given moment in time, reaches 34 kts to 63 kts (nhc.noaa.gov). Based on this criterion, storms that reached a maximum sustained wind speed of at least 34 kts, as recorded from land stations or data buoys located within 11 km of BCA, were included in this study. These stations or buoys included Fort Lauderdale Executive Airport (KFXE), Dania Pier (XDAN), Port Everglades (XPEG), South Port Everglades (PEGF1), Port Everglades Channel (PVGF1), and the Fort Lauderdale International Airport (KFLL). Although the wind strength measured during these storms may not directly cause impacts to BCA, the maximum sustained surface wind speed serves as a proxy for times of increased wave and surge energy that may have physically impacted BCA. The tropical storms and hurricanes that met the wind speed and distance criteria from 2003-2022 included Hurricane Frances and Jeanne (September 2004), Hurricane Katrina (August 2005), Hurricane Wilma (October 2005), Hurricane Isaac (August 2012), Hurricane Sandy (October 2012), Hurricane Irma (September 2017), Tropical Storm Gordon (September 2018), Hurricane Sally (September 2020), Hurricane Eta (November 2020), and Hurricane Elsa (July 2021). Nearly all selected events occurred after BCA data was collected that year; therefore, the effects of those events would have been documented during the next monitoring year. Only one storm, Hurricane Elsa, was an exception: it made landfall on July 7, 2021 in northern Florida, directly before SECREMP monitoring occurred on July 22, 2021.

Table 2. Tropical storm and hurricane wind strength data (nhc.noaa.gov) for each of the selected tropical storm and hurricane events. In cases where multiple stations/buoys gathered wind data, the values for maximum sustained surface wind and maximum sustained gusts were selected from the station/buoy that recorded the highest maximum sustained surface wind.

Storm	Date	Station	Max. Sustained Surface Wind (kts)	Max. Surface Gusts (kts)
Frances	September 5, 2004	KFXE	36	48
Jeanne	September 26, 2004	KFLL	35	49
Katrina	August 25, 2005	KFLL	52	71
Wilma	October 24, 2005	KFLL	61	86
Isaac	August 27, 2012	XPEG	42	58
Sandy	October 25, 2012	PVGF1	36	46
Irma	September 10, 2017	XPEG	61	74
Gordon	September 3, 2018	PEGF1	42	49
Sally	September 12, 2020	XDAN	34	42
Eta	November 9, 2020	XPEG	51	59
Elsa	July 5, 2021	XDAN	35	41

Statistical Analyses

Generalized linear mixed models (GLMMs) were used to statistically analyze temporal changes in percent benthic cover of living *A. cervicornis*, dead *A. cervicornis*, and hardbottom from 2003-2022 using R software (R Core Team, 2021). A single binomial GLMM was created with stations per year as replicates (n = 80). In each model, percent cover was fitted as a continuous dependent variable, year was fitted as a categorical fixed effect, and station was fitted as a categorical random effect. The number of points per station was fitted as weights. Fitted models were validated using the package "DHARMa" (Hartig, 2022), with residual diagnostics conducted to detect overdispersion, zero-inflation, heterogeneity of variances, and temporal autocorrelation. To validate the models and correct for overdispersion, GLMMs analyzing temporal changes in living *A. cervicornis*, dead *A. cervicornis*, and hardbottom were fitted with a beta-binomial model (Harrison, 2015). Model validation of the beta binomial GLMM indicated no problems. Post-hoc pairwise comparisons of year-to-year changes in the response variable were conducted using the package "emmeans" and Tukey method (Lenth, 2023). Emmeans linear contrasts were used to assess significant variation in levels of a fixed effect against the mean value.

Multivariate analyses were performed to assess temporal changes in benthic community structure and non-*A. cervicornis* stony coral community structure using Primer 7 (Clarke & Gorley, 2006). Benthic community structure was assessed as percent benthic cover per station per year. Non-*A. cervicornis* stony coral community structure was assessed as abundance of each species per station per year. Before analysis, each dataset was square-root transformed to reduce the influence of abundant taxa and enable rarer taxa to contribute to the similarity calculation. After this, a Bray-Curtis similarity matrix was generated. To analyze significant differences in benthic and coral community structure between years, analysis of similarity tests (ANOSIM) was performed with each station in each year as a replicate (9999 permutations). This analysis focused on major periods of change in community structure between consecutive years or major periods of change in community structure over multiple years. To assess significant temporal grouping structure within the benthic and coral communities, mean benthic and coral community structure per year were analyzed using similarity profile analyses (SIMPROF; 9999 permutations, 95% similarity between samples). A similarity percentage (SIMPER) analysis was performed to identify which species, taxa, or substrate types were driving differences between SIMPROF groups and years. From the SIMPER analysis, the taxa that cumulatively explained 50% dissimilarity between groups were selected. Temporal variation in benthic or coral community structure was visualized using a non-metric multidimensional scaling (nMDS) plot, where each sample represents mean community structure per year. Vectors were overlayed to visualize the origin of differences between samples. SIMPROF groups were also overlayed onto each nMDS plot for visualization. Finally, non-*A. cervicornis* taxa that drove variability in the benthic community were further analyzed using a binomial GLMM for significant temporal changes in substrate utility using R software (R Core Team, 2021). The benthic taxa that drove variability in benthic community structure were percent cover of macroalgae growth on dead *A. cervicornis* and hardbottom and percent cover of CCA growth on dead *A. cervicornis* and hardbottom. Macroalgae on both substrate types and CCA growth on *A. cervicornis* were fitted with a beta-binomial model due to overdispersion and only CCA growth on hardbottom was fitted into a binomial distribution with a zero-inflation parameter. Model validation and post-hoc analysis was conducted as previously described.

The density of the stony coral *Agaricia agaricites* and all other non-*A. cervicornis* stony coral from 2012-2022 were analyzed using Poisson GLMMs. *Agaricia agaricites* and all other non-*A. cervicornis* abundance were fitted as a continuous dependent variable, year was fitted as a categorical fixed effect, station was fitted as a categorical random effect, and the area of each transect was used as an offset term. Model validation and post-hoc analysis was conducted as previously described.

Results

Acropora cervicornis

Mean (± SE) live *Acropora cervicornis* cover in BCA was highest in 2004 (41.4% ± 1.3%) and declined over the study period from 34.8 ± 2% in 2003 to 2.4 ± 0.6% in 2022 (Figure 1). The 11 tropical storms and hurricanes, four heat stress events, and one cold stress event that occurred during the 20-year study coincided with periods of live coral cover decline (Figure 1). Notable periods of live cover decline included 2004 (41.4% ± 1.3%) to 2006 (22.8% ± 1.6%), 2008 (28.4% ± 0.93%) to 2011 (13.7% ± 1.2%), and 2012 (15.05% ± 1.65%) to 2016 (4.4% ± 0.97%). Significant consecutive annual declines occurred from 2005-2006 (GLMM, Tukey pairwise comparisons, $p < 0.0001$), 2010-2011 (GLMM, Tukey pairwise comparisons, $p = 0.044$), and 2015-2016 (GLMM, Tukey pairwise comparisons, $p = 0.0038$). From 2004 to 2006, four hurricanes (Jeanne, Frances, Wilma, and Katrina), and from 2012 to 2016, two hurricanes (Isaac and Sandy), passed near BCA. Heat stress events were documented in 2005, 2009, 2014, and 2015 and a cold stress event was documented in 2010. Significantly high disease was recorded at BCA in 2012 and significantly high disease and predation prevalence on *A. cervicornis* in BCA was recorded in 2015 at BCA (Goergen *et al.*, 2019), further contributing to the cover loss between 2015 and 2016. Live cover in 2018 (1.8% ± 0.4%) had significantly lower cover than 2020 (5.1% ± 1.2%) (GLMM, Tukey pairwise comparisons, $p < 0.05$), and this was the only year-to-year comparison in which an earlier year had significantly lower cover than a later year.

Dead *A. cervicornis* cover during the study period generally increased from 2003 to 2016, but decreased after 2017 (Figure 1). Mean (± SE) dead *A. cervicornis* cover increased from a low of 23.5% ± 3.2% in 2003 to a high in 2017 (80.3% ± 1.3%) and then decreased to 65.8% ± 6.9% in 2022. The greatest significant consecutive year-to-year increase in dead *A. cervicornis* cover occurred from 2005 (31.8 ± 2.9%) to 2006 (51.3 ± 3.5%) (GLMM, Tukey pairwise comparisons, $p = 0.0025$). Dead *A. cervicornis* cover declined from 2017 to 2022, and 2017 cover was significantly different than 2022 (Tukey pairwise comparisons, $p = 0.046$).

Hardbottom cover declined with declining live *A. cervicornis* cover and increasing dead *A. cervicornis* cover until 2015-2017, when hardbottom cover began to increase (Figure 1). Mean (± SE) hardbottom cover was greatest in 2003 (41.6 ± 4.5%), lowest in 2015 (13.6 ± 3.3%), and then increased to 31.8 ± 6.5% in 2022. Hardbottom cover was significantly greater in 2003 than 2017 (GLMM, Tukey pairwise comparisons, p = 0.0003), and cover was significantly lower in 2015 than 2022 (GLMM, Tukey pairwise comparisons, p = 0.012).

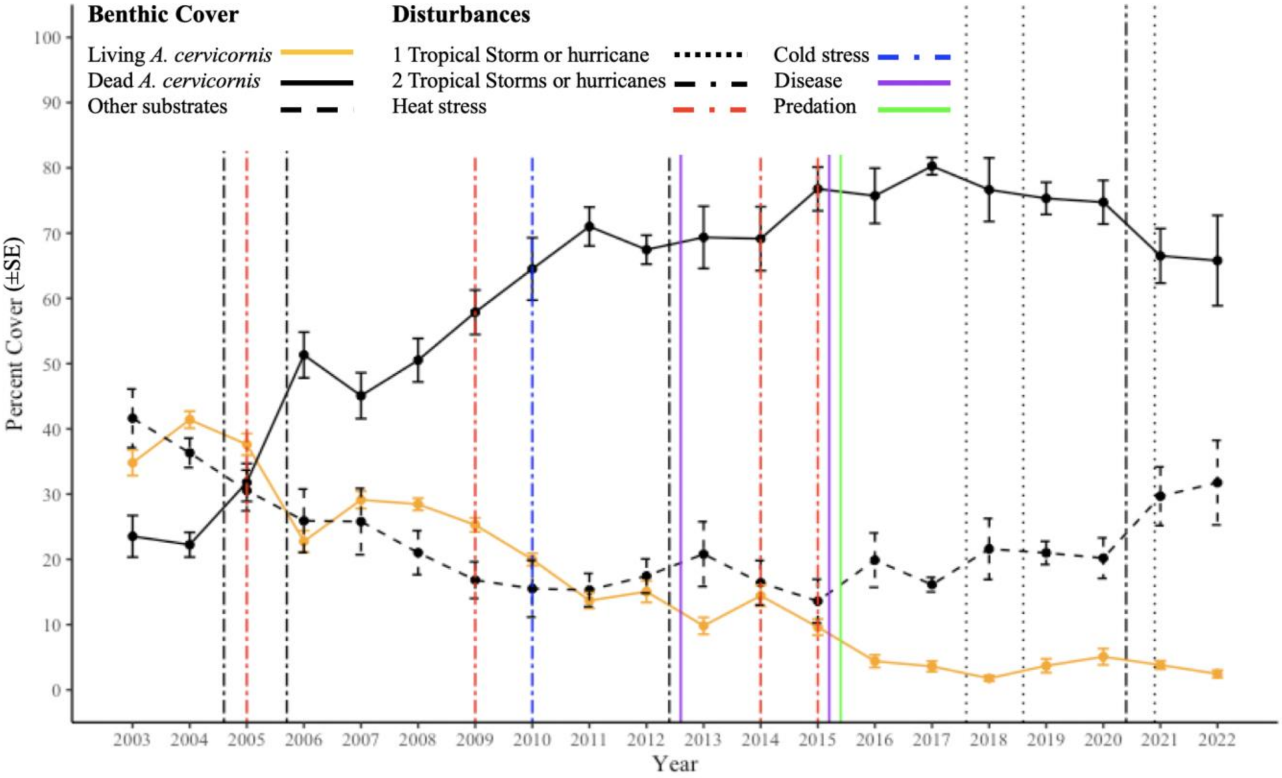

Figure 1: Annual mean (± SE) percent benthic cover of living *A. cervicornis*, dead *A. cervicornis*, and hardbottom (horizontal lines) and documented disturbance events (vertical lines). Tropical storm and hurricane information was taken from nhc.noaa.gov. The tropical storms and hurricanes included Frances and Jeanne (2004), Katrina and Wilma (2005), Isaac and Sandy (2012), Irma (2017), Gordon (2018), Sally and Eta (2020), and Elsa (2021). Other disturbance events included 2005 heat stress (Eakin *et al*., 2010; Wilkinson & Souter, 2008), 2009 high SST at BCA (Goergen *et al*., 2019), 2010 cold stress (Lirman *et al*., 2011; Jones *et al*., 2020), 2012 higher disease incidence at BCA (Goergen *et al*., 2019), 2014 and 2015 heat stress (Goergen *et al*., 2019; Jones *et al*., 2020), and 2015 disease and predation events at BCA (Goergen *et al*., 2019). Years in which there was one tropical storm or hurricane are represented by a black dotted line and years in which there were two are represented by a black dashed line.

Benthic Community

Benthic community structure significantly changed from 2003 to 2022, coinciding with declines in live *A. cervicornis* and changes in substrate availability (Figure 2). Three periods of significant change in benthic community structure were identified. From 2005-2006, there was significant change in benthic community structure (ANOSIM, p = 0.03) driven by decreases in live *A. cervicornis* and hardbottom cover and increased dead *A. cervicornis* cover (SIMPER, cumulative percent contribution = 51.72%). Benthic community structure significantly changed from 2008-2010 (ANOSIM, p = 0.03), where variability was driven by decreases in live *A. cervicornis* and increases in dead *A. cervicornis* and macroalgae and CCA growing on dead *A. cervicornis* (SIMPER, cumulative percent contribution = 51.10%). Finally, benthic community structure significantly changed from 2019-2021 (ANOSIM, p = 0.03), when dead *A. cervicornis* cover declined, CCA and macroalgae cover on dead *A. cervicornis* increased, and hardbottom and macroalgae growing on hardbottom increased (SIMPER, cumulative percent contribution = 52.7).

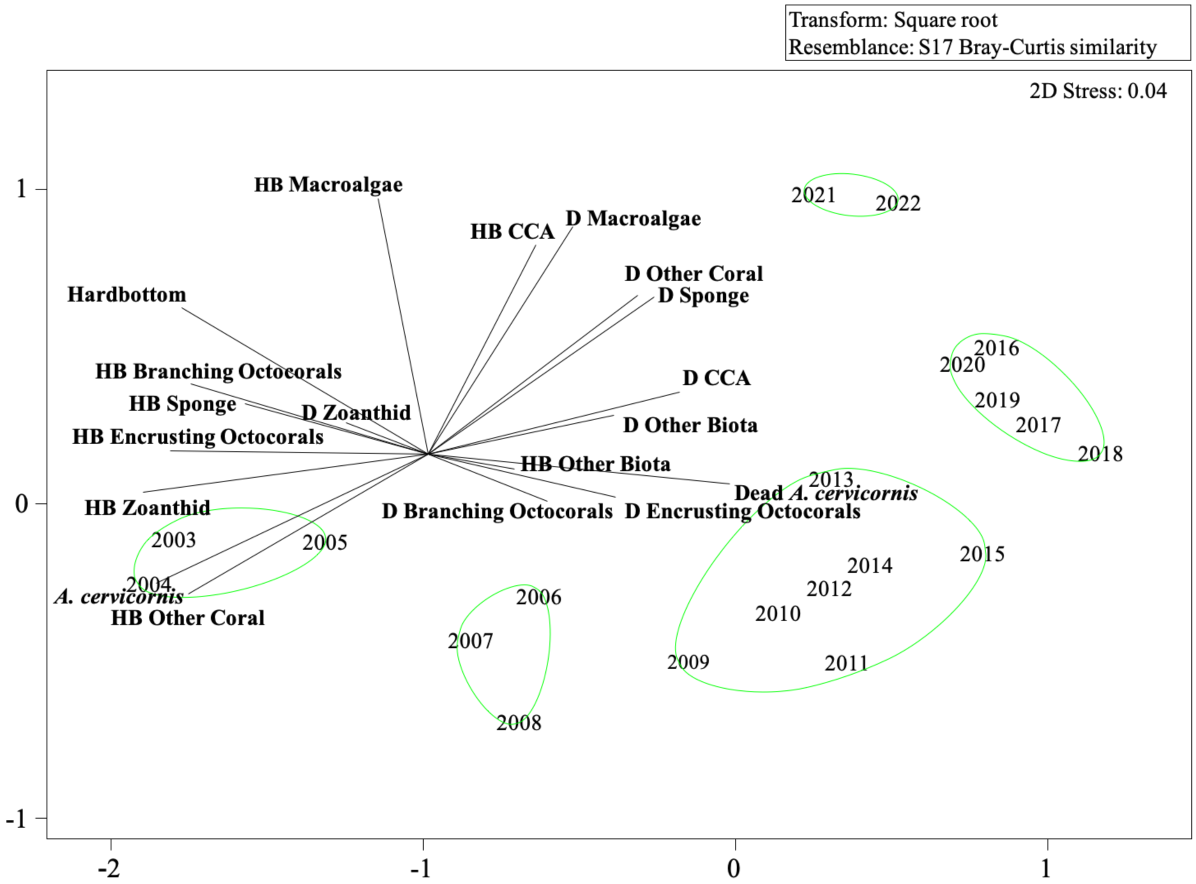

Figure 2. nMDS plot of benthic community structure based on the percent benthic cover over time. Vectors represent benthic community taxa separated by the types of substrates they were recorded growing on. The "D" in front of taxa labels denotes "percent cover of this taxon growing on dead *A. cervicornis*" and the "HB" denotes "percent cover of this taxon growing on hardbottom". The two different substrates observed with nothing but turf algae growth are also displayed (dead *A. cervicornis* and hardbottom). Green circles identify significant groups from SIMPROF analysis.

SIMPROF analysis identified five groups of years that varied significantly (SIMPROF, $p = 0.001$). The five groups generated were 2003-2005, 2006-2008, 2009-2015, 2016-2020 and 2021-2022. 2003-2005 had higher *A. cervicornis* and hardbottom cover and lower dead *A. cervicornis* cover compared to 2006-2008 (SIMPER, cumulative percent contribution = 56.75%). 2006-2008 had higher *A. cervicornis* and hardbottom cover than 2009-2015, which had higher dead *A. cervicornis* and macroalgae growth on dead *A. cervicornis* cover (SIMPER, cumulative percent contribution = 54.77%). Macroalgae cover on dead *A. cervicornis* significantly increased from 2008-2013 (GLMM, Tukey pairwise comparisons, $p = 0.017$) and had a significantly higher percent cover in 2013 (GLMM, emmeans linear contrasts, $p = 0.0202$) (Figure 3). Variability between SIMPROF groups 2009-2015 and 2016-2020 was driven by a further decline in *A.*

cervicornis and increases in hardbottom, macroalgae growing on dead *A. cervicornis*, and CCA growing on dead *A. cervicornis* (SIMPER, cumulative percent contribution = 55.46%). This is supported by significant increases in macroalgae on dead *A. cervicornis* from 2009-2016 (GLMM, Tukey pairwise comparisons, $p = 0.045$) and 2009-2020 (GLMM, Tukey pairwise comparisons, $p = 0.05$) and significantly higher benthic cover in 2016 (GLMM, emmeans linear contrasts, $p = 0.0001$). CCA growth on dead *A. cervicornis* was significantly higher in 2015 and 2017-2019 (GLMM, emmeans linear contrasts, $p < 0.05$) compared to other years. The variability between SIMPROF groups 2016-2020 and 2021-2022 was driven by a decline in dead *A. cervicornis* and increases in hardbottom, macroalgae growth on dead *A. cervicornis*, and macroalgae growth on hardbottom (SIMPER, cumulative percent contribution = 59.86%). This is supported by significant increases in macroalgae growth on hardbottom from 2017-2022 (GLMM, Tukey pairwise comparisons, $p = 0.023$) as well as having significantly higher benthic cover in 2018, 2021, and 2022 (GLMM, emmeans linear contrasts, $p < 0.05$) compared to other years. Macroalgae growth on dead *A. cervicornis* significantly increased from 2018-2021 (GLMM, Tukey pairwise comparisons, $p = 0.0005$) and had significantly higher cover in 2017, 2020, 2021, and 2022 (GLMM, emmeans linear contrasts, $p < 0.05$).

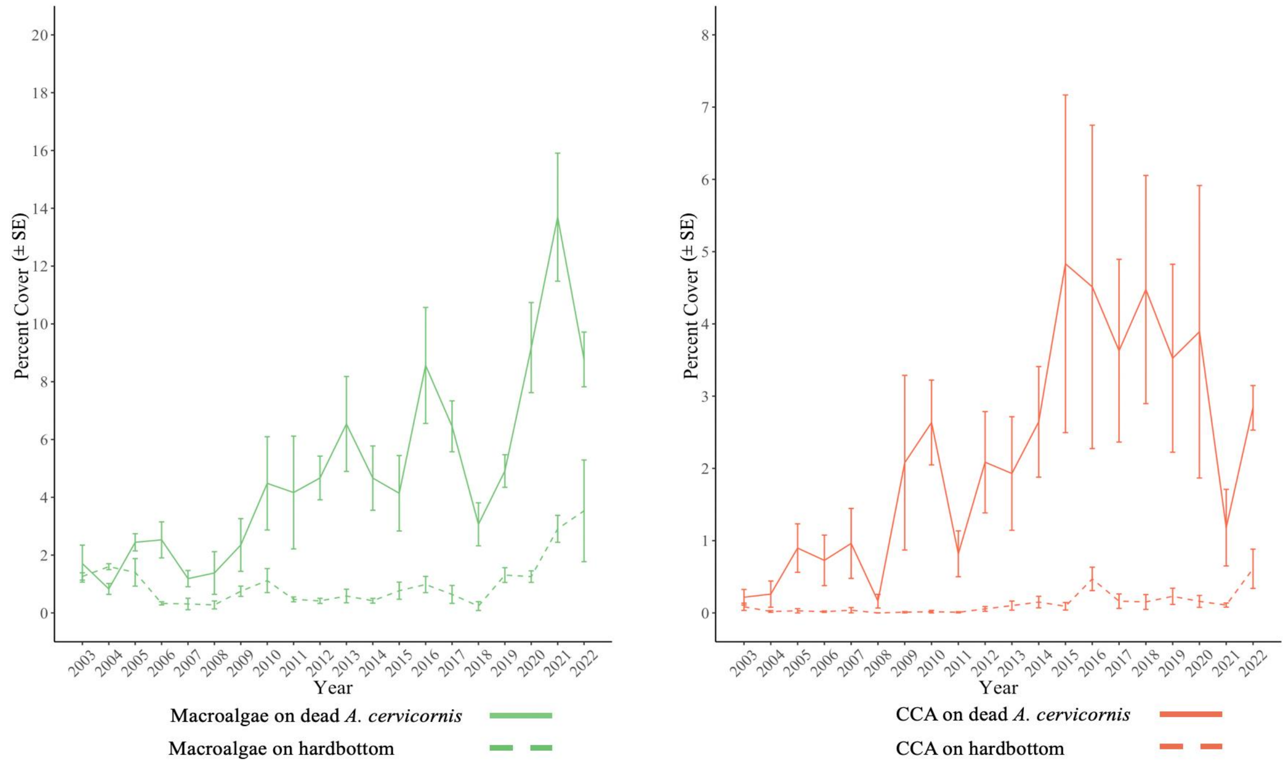

Figure 3. Percent benthic cover of macroalgae and CCA divided into percent cover of substrate types they were recorded on from 2003-2022. The taxa selected explained much of the variability in benthic community structure throughout the study period according to ANOSIM and SIMPROF analysis.

The non-*A. cervicornis* stony coral community exhibited significant change from 2012-2022 (Figure 4). Two periods of significant change in stony coral community were detected (ANOSIM, *p* = 0.03), 2014-2016 (SIMPER, cumulative percent contribution = 74.13%) and 2016-2019 (SIMPER, cumulative percent contribution = 56.88%). Both changes were driven by *A. agaricites* density. There were frequent increases in *A. agaricites* density, with significant inter-annual increases from 2014-2015 (GLMM, Tukey pairwise comparisons, *p* = 0.008), 2016-2017 (GLMM, Tukey pairwise comparisons, *p* <0.0001), and 2019-2020 (GLMM, Tukey pairwise comparisons, *p* = 0.008) (Figure 5). Two SIMPROF groups were identified, 2012-2016 and 2017-2022 (Figure 4). The differences between groups were again largely driven by increases in *A. agaricites* (SIMPER, cumulative percent contribution = 59.24%). *Agaricia agaricites* significantly increased in density from 2012-2022 (GLMM, Tukey pairwise comparisons, *p* = <0.0001) and shifted from below average density in 2016 to significantly higher average density in 2017 (GLMM, emmeans linear contrasts, *p* = <0.0001). *Agaricia agaricites* did experience a significant decrease in density from 2020-2021 (GLMM, Tukey pairwise comparisons, *p* = <0.0001).

Although *A. agaricites* drove all variability in the non-*A. cervicornis* stony coral community, other species of non-*A. cervicornis* stony coral shifted to above average density from 2017 to 2018 and had significantly higher average density in 2020, 2021, and 2022 (GLMM, Tukey pairwise analysis, p = <0.05) compared to other years.

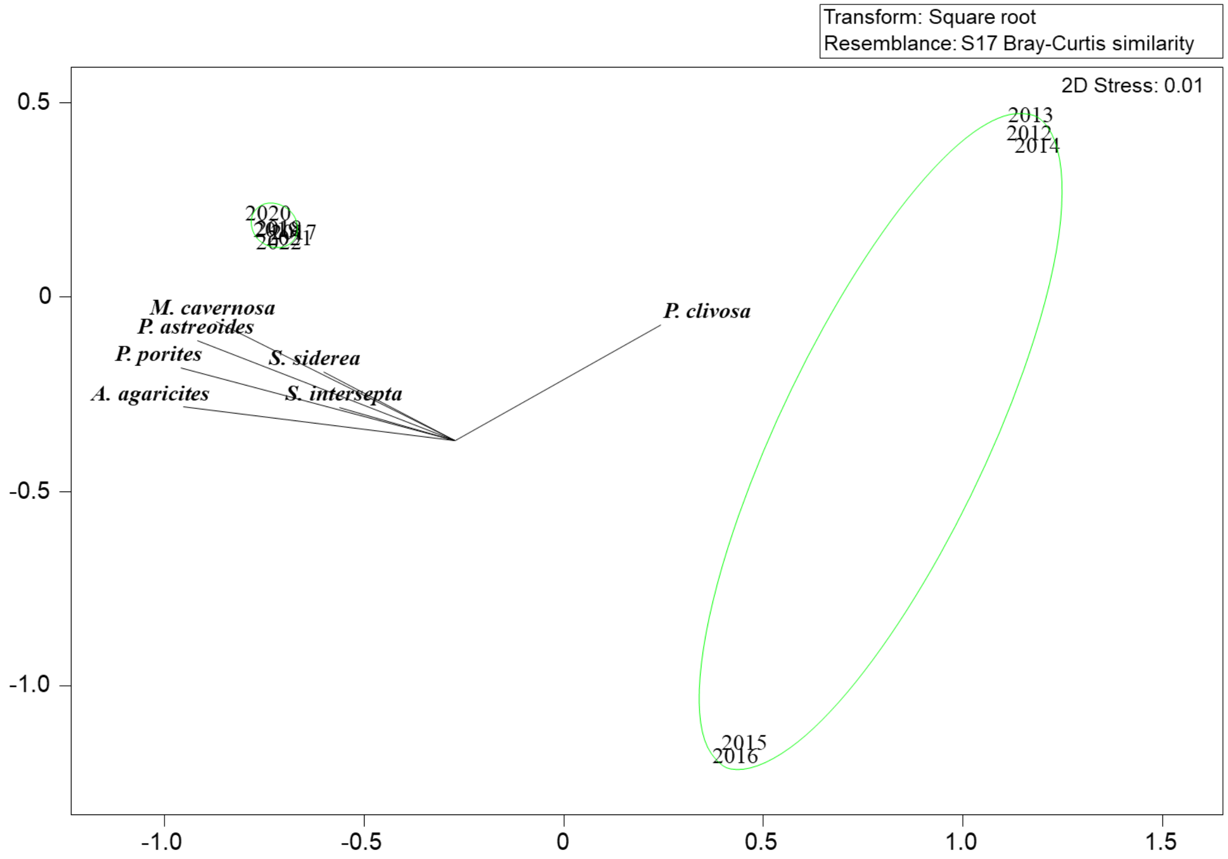

Figure 4. nMDS plot comparing the mean density of the non-*A. cervicornis* stony coral community over time. Green circles identify significant groups from SIMPROF analysis.

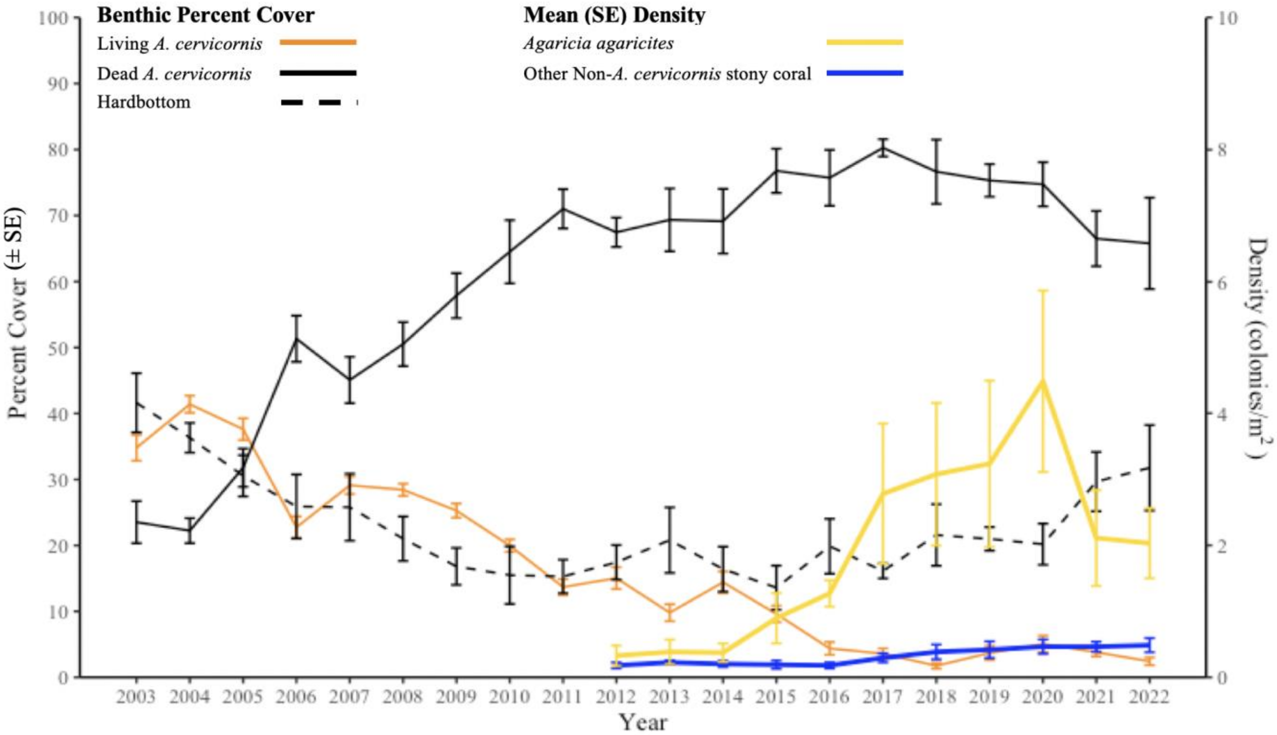

Figure 5. Percent benthic cover of living *A. cervic*ornis, dead *A. cervicornis*, and hardbottom from 2003-2022 and mean density (± SE) of *Agaricia agaricites* and other non-*A. cervicornis* stony corals excluding *Agaricia agaricites* from 2012-2022.

Discussion

BCA live *A. cervicornis* cover declined by 93% during this 20-year study, primarily attributed to both acute and chronic disturbances including heat stress, cold stress, disease, predation, and tropical storms and hurricanes. These disturbances gave limited opportunities for recovery, resulting in a prolonged period of decline, and drove significant shifts in substrate type within the study site. Annual temporal changes in macroalgae and CCA benthic cover in relation to changes in substrate cover, as well as the increases of the brooding stony coral species *A. agaricites*, further highlight changes in the benthic community due to impacts of disturbance. Despite continuous loss of living *A. cervicornis* in the thicket, standing dead *A. cervicornis* branches continued to provide unique functional services for these benthic taxa. However, because these benthic taxa are not contributing to the dead *A. cervicornis* framework, ongoing disturbances and the mechanical and biological degradation of dead branches results in the gradual loss of the unique functional services provided by BCA, ultimately transforming the environment into a hardbottom-dominated habitat. Continued monitoring efforts will likely capture the complete collapse of this functionally important habitat as disturbances persist.

Nearly 20 documented disturbance events impacted BCA over 20 years, and the timing of these disturbances were often followed by significant changes in live *A. cervicornis*, dead *A. cervicornis*, and hardbottom benthic cover. Declines in live cover were mostly gradual except for those observed following the 2005 hurricane season and the 2014-2016 heat stress. Tropical storms and hurricanes have been known to cause immediate mechanical damage to coral reefs after impact (Gardner *et al.*, 2005; Eakin *et al*., 2010) and recovery to pre-hurricane cover can take up to eight years (Gardner *et al*., 2005). Hurricane Lenny severely damaged reefs in Curacao and Bonaire in 1999, having a greater impact on branching and plating species (Bries *et al.*, 2002). Brewers Bay reef in St. Thomas was impacted by Hurricane Earl and heat stress in 2010, causing mass fragmentation, coral bleaching, and disease (Brandt *et al*., 2013). The hurricanes selected in this study have also been implicated in coral reef loss in South Florida. Hurricane Wilma and Katrina were associated with sediment resuspension and cold-water upwelling that affected the FCR (Collier *et al.*, 2008), Hurricane Isaac contributed to high fragmentation and elevated disease occurrence at BCA (Goergen *et al*., 2019) and Hurricane Irma contributed to the dislodging of many *A. cervicornis* colonies (Walker, 2018).

Other decreases in live *A. cervicornis* cover occurred concurrently with disturbances found in the literature review, such as heat stress, cold stress, and significant predation and disease. *Acropora cervicornis* is known to be particularly susceptible to cold stress (Porter *et al.*, 1982). *Acropora* spp. have lost 95% of colonies after heat stress events on the Great Barrier Reef (Berkelmans & Oliver, 1999) and Acroporidae declines have been associated with heat stress along the FCR (Jones *et al*., 2020). Live *A. cervicornis* cover at BCA is affected by temperature and has shown seasonal variations (Walker *et al.*, 2012). The hottest years on record for reefs in South Florida (Manzello, 2015) were reported in 2014 and 2015, which corresponds to our observation of significant losses in cover during that time. Additionally, disease has greatly affected *A. cervicornis* and is a principal driver of mortality in many areas of the Caribbean (Aronson & Precht, 2001). BCA specifically has experienced declines in *A. cervicornis* cover due to disease (Goergen *et al.,* 2019); the source of disease is unknown but may be caused by other disturbances such as predation (Renzi *et al.*, 2022), heat stress (Rogers *et al.*, 2009), and tropical storms and hurricanes (Knowlton *et al.*, 1981). Predation played a major role in declines of *A. cervicornis* in

Jamaica after the passing of Hurricane Allen (Knowlton *et al*., 1990) and significant predation in 2015 at BCA contributed to declines in *A. cervicornis* as well (Goergen *et al.,* 2019). The evidence suggests that the sheer number, variety, and frequency of disturbances that have impacted BCA are likely linked to observed reductions in *A. cervicornis* cover.

Despite rapid growth rates relative to other stony coral species, *A. cervicornis* at BCA faces limitations in recovering from disturbances. Significant recovery was only seen in the 2018-2020 period when live *A. cervicornis* cover significantly increased coinciding with a period of less disturbance. This recovery period was followed by significant *A. cervicornis* cover loss in 2020-2022 associated with more tropical storms and hurricanes. Recovery may be facilitated by *A. cervicornis* colony growth, reattachment and successful growth of loose fragments, and successful larval recruitment. However, both reattachment success of loose fragments and *A. cervicornis* larval recruitment in this area have previously been found to be very low (Vargas-Angel *et al.*, 2006; Goergen *et al.*, 2019). Additionally, within the Coral ECA, frequent disturbances have limited stony coral growth, even in areas with lower chronic pressure (Jones *et al.*, 2022). Despite some brief instances of recovery, chronic disturbance at BCA will likely limit the potential for significant recovery of this thicket.

As a result of chronic disturbance, hardbottom and dead *A. cervicornis* cover changed throughout the study. Dead *A. cervicornis* cover exceeded living *A. cervicornis* cover after the passing of Hurricanes Wilma and Katrina in 2005, two of the more powerful storms documented during the study period. Dead *A. cervicornis* branches fragmented and remained in the thicket on the substrate as rubble, increasing in percent cover and consequently decreasing the percent cover of hardbottom. Although this study did not differentiate between rubble and dead *A. cervicornis* in the image analysis, in many years, the loss of living *A. cervicornis* percent cover was not proportional to the increase in dead *A. cervicornis* cover. For example, from 2008 to 2009 there was a 3.1% decrease in living *A. cervicornis* cover, while there was a 7.4% increase in dead *A. cervicornis*, which is more than double the loss in living *A. cervicornis* and because *A. cervicornis* cover was decreasing throughout the earlier years of the study, hardbottom percent cover was decreasing due to increases in the dead *A. cervicornis,* not living *A. cervicornis*. It would be expected that if rubble was not being generated, then living *A. cervicornis* cover and dead *A. cervicornis* cover would be inversely proportional to each other while hardbottom would remain relatively stable. The constant movement of rubble prevents attachment and binding, creating an unstable environment and making it difficult for benthic taxa to grow on both the rubble itself and the hardbottom underneath (Kenyon *et al.*, 2023). As a result, utilization of dead *A. cervicornis* stable structure was greater as rubble covered the hardbottom and living *A. cervicornis* died. Significant declines in dead *A. cervicornis* cover after the passing of Hurricane Irma in 2017 and through 2022 indicate that physical disturbance and bio-erosional processes continued the breakdown of stable dead *A. cervicornis* structure. Toward the end of the study, living *A. cervicornis* cover remained low while there were decreases in dead *A. cervicornis* and increases in hardbottom cover (i.e., revealing more hardbottom in images), which is likely explained by displacement of rubble off transect. Prior research has shown that acroporid rubble can be moved, on average, 33 cm in calmer periods and as much as 149 cm in windier conditions (defined as upwards of 20 kts) at sites with a similar depth as BCA (Cameron *et al.*, 2016). The westward movement of live *A. cervicornis* cover was measured at BCA between 2008 and 2011 (Walker et al 2012); therefore, it is likely that dead colonies could be moved as well. More tropical storms and hurricanes passed near BCA toward the end of the study, likely contributing to the consistent decrease in dead *A. cervicornis* cover and mobilization of unconsolidated rubble.

The loss of live *A. cervicornis* cover left more substrate to be colonized and allowed other benthic taxa to increase in cover. Macroalgae and CCA increased in percent cover between 2009-2022 on both types of substrates, but mostly on dead *A. cervicornis*. Macroalgae increases have been reported in many reef ecosystems throughout the Caribbean (Aronson & Precht, 2001; Hughes *et al.*, 2010; García-Urueña & Garzón-Machado, 2020; Jones *et al.*, 2022). Coral reefs in the Coral ECA have struggled to maintain stony coral cover and much of the space they once occupied has been replaced by macroalgae (Jones *et al.*, 2022). Macroalgae can also affect recruitment success and cause mortality through abrasion on stony coral (Box & Mumby, 2007). Macroalgae have been noted to reduce recovery of *A. cervicornis* (García-Urueña & Garzón-Machado, 2020). Research has shown that macroalgae cover in the past has dominated cover along the hardbottom nearshore ridge complex of South Florida (Banks *et al*., 2008) and cover is expected to increase (Jones *et al.*, 2020). Without *A. cervicornis* growth driving thicket recovery, benthic taxa such as macroalgae will increase in cover, and these sites will evidently resemble nearshore hardbottom habitat found throughout the Coral ECA.

Although non-*A. cervicornis* stony coral density increased in between most monitoring periods, this increase was dominated by small, brooding *A. agaricites* that do not provide the same functional services that *A. cervicornis* provided. *Agaricia agaricites* experienced a significant increase in density from 2014-2020. *Agaricia agaricites* contributed to 91% of the total non-*A. cervicornis* stony coral density at its highest density in 2020, and over 87% of density between 2016-2020. During this time, dead standing *A. cervicornis* in BCA provided a complex structural environment. *Agaricia agaricites* is known to colonize shaded regions of the reef, including within the understory of *A. cervicornis* dead structure (Orrell, 1981). It has probably always existed within BCA, but as *A. cervicornis* died leaving more dead structure, more substrate was available to colonize. Being a brooding species, *A. agaricites* can colonize disturbed reef environments quickly (Robbart *et al.*, 2004). Other brooding species, such as *P. astreoides* and *Porites porites*, were also abundant. Research has shown that increases in species such as *A. agaricites* and *P. astreoides* do not properly sustain reef functionality and structure (Alvarez-Filip *et al*., 2013); therefore, they likely could not maintain the stable dead *A. cervicornis* or bind unconsolidated rubble at BCA. After the steep decline in dead *A. cervicornis* cover from 2020-2021, there was also a steep decline in *A. agaricites* density, as constant tropical storm and hurricane disturbance further collapsed the dead structure. Although there was an increase in non-*A. cervicornis* stony coral density, this increase was dominated by *A. agaricites* which could not bind and sustain the structure built by *A. cervicornis* after the passage of several tropical storms and hurricanes toward the end of the study.

The annual nature of the data collection and the specific disturbances analyzed may not fully explain the changes in the benthic community structure seen in this study. Water quality (De'ath & Fabricius, 2010), effects of pollution (Finkl & Charlier, 2003), and presence/absence of herbivores (Hughes *et al.*, 2010) may be additional drivers of change. Some acute disturbances may not have been captured in the point count images or literature: for example, there were reports of a cyanobacteria, *Lyngbya* spp., bloom at BCA in 2004 (Wheaton *et al.*, 2007) that were not captured by the image analysis. More frequent monitoring, similar to the tri-annual monitoring utilized by Goergen *et al.*, 2019, can aid in detection of various acute disturbances. It is probable that BCA was affected by much more than the 19 disturbances recorded from this study.

Acropora cervicornis thickets, including BCA, provide unique functional services. When an *A. cervicornis* thicket is healthy with sustained growth that can recover from disturbance, it provides a three-dimensional structure for fish and invertebrates to utilize as habitat. Long-term structure is only maintained by *A. cervicornis* growth. The live cover at BCA was not sustained in the thicket due to chronic disturbances inhibiting recovery; however, dead structure was documented to remain for years after significant loss of live cover. Therefore, the loss of live cover did not indicate a loss in all functional services. The dead framework continued to provide the benefits of its branching structure for years. However, without living *A. cervicornis* to create new structure, these services will be lost as a result of chronic and acute disturbances impacting BCA. The loss of complex architectural structure is known as reef-flattening and is a phenomenon documented in the wider Caribbean (Alvarez-Filip *et al.*, 2009b). When these habitats are lost, there are fewer niches for organisms, which reduces functional services and decreases biodiversity. This can lead to a process known as biotic homogenization, where species assemblages become more similar at different locations over time and is an ongoing occurrence along the FCR (Burman *et al.*, 2012). The long-term persistence of *A. cervicornis* thickets, even in the form of dead structure, underscores their irreplaceable role in providing essential functional services in the Coral ECA, and the urgent need for conservation and restoration efforts to prevent further loss of these unique habitats.

The sheer number, variety, and frequency of disturbances that BCA has experienced has limited the recovery potential of *A. cervicornis* and the unique services this thicket provides. A lag between decreases in live *A. cervicornis* and dead *A. cervicornis* provided habitat for other benthic taxa to colonize, but continued disturbance has led to its breakdown, ultimately resulting in a decrease in percent cover of dead *A. cervicornis* toward the end of the study. The movement of rubble generated by tropical storms and hurricanes may contribute to the potential homogenization of BCA in the future, resembling hardbottom habitats in the Coral ECA nearshore environment. It is likely that continued monitoring efforts will capture the complete collapse of this functionally important habitat. It will prove difficult to maintain ecosystems like BCA, as many of the disturbances are caused by larger, global issues such as climate change. Mitigating local stressors can help and restoration of *A. cervicornis* can also be used as a tool, at least until more sweeping actions are taken to improve environmental conditions (Miller *et al.*, 2016; Goergen & Gilliam, 2018; Goergen *et al.*, 2019). The importance of *A. cervicornis* is widely recognized and thus it is a frequent target in restoration efforts, in which many practitioners have had success in propagating and outplanting the species (Schopmeyer *et al.*, 2017). This study highlights the vulnerability of BCA and the importance of considering the cumulative impacts of multiple disturbances in understanding coral reef dynamics and recovery potential. Further research and conservation efforts are needed to mitigate the impacts of compound disturbances and support the recovery of *A. cervicornis* and other stony coral species in BCA and similar ecosystems.

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