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SHORT—TERM TEMPORAL TRENDS OF A CORAL REEF IN SAMANA (DOMINICAN REPUBLIC): THE VALUE OF A PERMANENT MONITORING PROGRAM TO IDENTIFY DRIVERS OF RAPID CHANGE§

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Abstract: Permanent monitoring programs are valuable to identify drivers of ecosystem trends. For example, in 2021, we reported the first record of Stony Coral Tissue Loss Disease (sctld) along the northeastern coast of the Dominican Republic, affecting major reef—building coral species with a prevalence above 30%. However, a few sites such as Carenero remained unaffected by sctld for almost 2 years. The average coral cover in this site was about 18—25% (mean 18.3% ± sd 1.5), and disease prevalence did not exceed 7% in the coral community. During the first quarter of 2022, a few colonies (<1%) of *Montastraea covernosa, Pseudodiploria strigosa* and *Colpophyllia natans* started to show macroscopic signs of sctld and between April and September of that year, average prevalence of sctld increased 4—fold. In September 2022, Hurricane Fiona affected the Dominican Republic, hitting the island's eastern coast and moving northwest. Coral diseases such as sctld and Caribbean Yellow Band Disease (CYBD) increased in prevalence, reaching up to 36% among the top 5 coral reef—building species and the average of dead colonies reached 43%. We recorded a 3—fold reduction of average live coral cover (77% lost) by the end of 2022, with *Orbicella faveolata, M. covernosa, C. natans* and *P. strigosa* the most affected species. Furthermore, Fiona lifted and turned upside down large *O. faveolata* colonies, particularly in the reef flat, and severely affected a large thicket of *Acropora cervicornis*. Results highlights the value of recurrent and permanent monitoring programs to identify stressors affecting coral reefs.

Resumen: Los programas de monitoreo permanente son útiles para identificar las tendencias en los ecosistemas. En 2021, reportamos el primer registro de la enfermedad de pérdida de tejido rápido (sctld) en la costa noreste de la República Dominicana sobre los principales constructores de arrecifes con una prevalencia superior al 30%. Sin embargo, algunos sitios como Carenero no se vieron afectados por sctld durante casi 2 años. La cobertura media de coral en este sitio oscilaba entre 18—25% (media del 18,3% ± sd 1,5), y la prevalencia de la enfermedad en la comunidad no superó 7%. A principios de 2022, algunas colonias (<1%) de *Montastraea covernosa, Pseudodiploria strigosa,* y *Colpophyllia natans* mostraron signos de sctld y entre abril—septiembre, la prevalencia promedio de sctld se cuadruplico. En septiembre 2022, el huracán Fiona afectó a la República Dominicana, desde el este y desplazándose hacia el noroeste. Las enfermedades, como la sctld y la banda amarilla (CYBD), aumentaron en prevalencia alcanzando hasta el 36% entre las cinco principales especies constructoras arrecifales lo que incremento el porcentaje de colonias muertas a 43%. A finales de 2022 registramos una reducción de 3 veces de la cobertura media de coral vivo (77% perdida), siendo *Orbicella faveolata, M. covernosa, C. natans* y *P. strigosa* las especies más afectadas. Además, Fiona levantó y volteó grandes colonias de *O. faveolata*, y afectó severamente a *Acropora cervicornis*. Los resultados destacan el valor de los programas de monitoreo recurrentes y permanentes para identificar los factores de estrés que afectan a los arrecifes de coral.

Key words: sctld, coral diseases, impact, coral reef decline, hurricane

Introduction

Since the late 1990's, coral reef scientists have recognized the Caribbean region as a hotspot of coral diseases (Green and Bruckner 2000, Weil 2004, Weil et al. 2006). Local and regional monitoring programs have shown that coral disease epizootic events have changed the structure and function of reefs across the region, as new diseases appear and other conditions continue to spread rapidly while populations of major reef builders are declining (Aronson and Precht 2001, Alvarez—Filip et al. 2022). Historically, white diseases (i.e., conditions that lead to rapid detachment of coral tissues from their skeletons) such as white band disease and white plague (type I and II), have produced unprecedented changes in the region (Weil 2004). Caribbean yellow band disease (CYBD) has likewise affected populations of *Orbicella annularis*, *O. faveolata* and *O. franksi* (Bruckner and Bruckner 2006, Bruckner and Riegl 2015), particularly larger colonies that both contribute to the bulk of live coral cover in the region and provide gametes and larvae every year as these colonies are sexually mature. Several studies have shown that coral diseases such as CYBD reduce the reproductive output of corals (Weil et al. 2009a). In consequence, the populations of major Caribbean coral reef—builders are currently at risk of extinction because they have reduced their numbers, shrunk their

§This manuscript is based on a presentation given at the 76th meeting of the Gulf and Caribbean Fisheries Institute in November 2023 in Nassau, The Bahamas

distribution and/or lost their habitats (Carpenter et al. 2008).

The stony coral tissue loss disease (sctld) epizootic event is the most recent recorded in the region. First noted in 2014 on Virginia Key (Miami) reefs (Precht et al. 2016), it has since rapidly spread, first along the Florida Keys and then across the Caribbean, affecting over 30 scleractinian species in more than 28 territories (https://www.agrra.org Coral Disease Outbreak – AGRRA) from shallow to mesophotic reef habitats (Williams et al. 2021). Sctld can trigger rapid shifts in the structure and function of Caribbean coral reefs, as several study cases from Mexico (Alvarez–Filip et al. 2019, 2022, Estrada–Saldívar et al. 2021), Florida (Hayes et al. 2022), the USVI (Brandt et al. 2021) and the Dominican Republic (Croquer et al. 2022a) have shown. These changes include the rapid demise of foundation species (e.g. *Dendrogyra cylindrus, Colpophyllia natans*, *Montastraea cavernosa*, *Pseudodiploria strigosa* and *Siderastrea siderea*) and common coral species (e.g. *Meandrina* spp, *Eusmilia fastigiata*, *Pseudodiploria clivosa*), as well as impacts on juvenile corals from several species (Croquer et al. 2022a), consequently decreasing alpha diversity and concomitantly losing structural complexity (Alvarez–Filip et al. 2022).

Coral diseases have also affected coral reef health in the Dominican Republic (Croquer et al. 2022a, Steneck and Torres 2023). Recent studies show that coral diseases such as Dark Spot Disease (DSD), CYBD and particularly sctld are widespread across the island, including inshore reefs and outer reef shelfs (e.g. Silver Bank), affecting major populations of reef–building corals and recruits at different spatial scales (Croquer et al. 2022a, Sellares–Blasco et al. 2023). Furthermore, according to Steneck and Torres (2023), diseases have played a major role in the rapid and recent decline of different coral reef health indicators across the island.

Hurricanes have also produced large impacts on coral reefs across the Caribbean region including the Dominican Republic (Goldenberg et al. 2001, Jury et al. 2012). With increasing force and frequency, hurricanes have been producing mechanical damages and reef flattening since the 1980's (Hughes 1994, Gardner et al. 2005) and they continue to be a destructive force for the reef carbonate framework (Heron et al. 2008). Recurrent category 5 hurricanes such as Irma and Maria produced devastating effects on reefs in various countries of the region (e.g. Florida, Puerto Rico, the West Indies and the USVI) (Rousseau et al. 2010, Gochfeld et al. 2020, Madden et al. 2023). In the Dominican Republic, Croquer et al. (2022b), Steneck and Torres (2023) and Sellares–Blasco et al. (2023) have identified hurricanes as a significant threat and one of the underlying drivers of rapid coral reef decline in Montecristi and the Silver Bank. However, in the country, there are few examples demonstrating the role of diseases and hurricanes on trajectories of coral decline based on frequent and permanent monitoring efforts.

In 2021, the Dominican Reef Network (RAD in Spanish) started a national collaborative monitoring program of both coral diseases and reef health indicators (e.g. coral cover, benthic community structure, abundance of fish, etc.). While various institutions have been significantly contributing with coral monitoring in the past, RAD's program includes various time points in the same year across the island, combining photoquadrats with belt–transects and AGRRA methods, with sampling conducted every quarter within each year. Thus, more frequent sampling allows for a more detailed description of temporal changes and trajectories of the benthic community structure in the country. In this paper, we present the case study of Carenero, a reef that has experienced rapid changes in benthic and coral assemblages. We aimed to highlight the importance of frequent and intensive monitoring programs to pinpoint the drivers of coral reef decline.

Materials and Methods

Study area

Carenero is a small rocky island inside Samana Bay and a Marine Protected Area (MPA) located on the northeastern coast of the Dominican Republic (Figure 1). The reef is fringing, narrow and shallow with a platform that extends windward from the shoreline along 80 m and a smooth slope reaching a maximum depth of 8–11 m. A large thicket of *Acropora cervicornis* covers extensive portions of the platform. Along the slope, there are about 15 scleractinian coral species; in deeper habitats, scattered coral and octocoral colonies are common. During coral disease monitoring surveys that started in 2021, Croquer et al. (2022a) catalogued the reef of Carenero as the healthiest inside Samana Bay due to the absence of sctld and other diseases compared to other locations, both inside and outside the bay.

Monitoring and field work

Coral disease and benthic community structure monitoring in Carenero started during the first quarter of 2022 and is currently ongoing. We conducted coral disease surveys following the protocol outlined by the Dominican Reef Network (Croquer et al. 2022a). Briefly, three 10 x 2 m (20 m^2) belt–transects were haphazardly deployed along the reef between 7–11 m to count every single coral colony by species and assigning each of the following categories to their condition: healthy, diseased by suspected type, paled/bleached, predated and other conditions including recently dead colonies.

In addition, we made high–resolution videos of the benthos over the same belt–transects using an underwater camera (Olympus TG6). From the videos, we extracted 10 to 15 images (every 4 to 5 seconds) using the multimedia framework ffmpeg (N–112324–g9240035c0e–tessus). Since coral diseases decrease live coral cover rapidly, particularly those that are virulent and affect a wide range of hosts (e.g. sctld), we used changes in coral cover and relative live coral cover as proxies of the impact of coral diseases in the study site. In addition, we used increases in algal cover and/or changes in other benthic groups as indicators of rapid change in benthic community structure. Finally, because it is impossible to diagnose coral diseases only from the field observations, we regarded all colonies showing specific macroscopic signs of diseases as "suspected cases".

The analysis of benthic images was conducted with the software PhotoQuad following the procedures outlined by Miyazawa et al. (2020). Briefly, from each image, we drew an 80 x 90

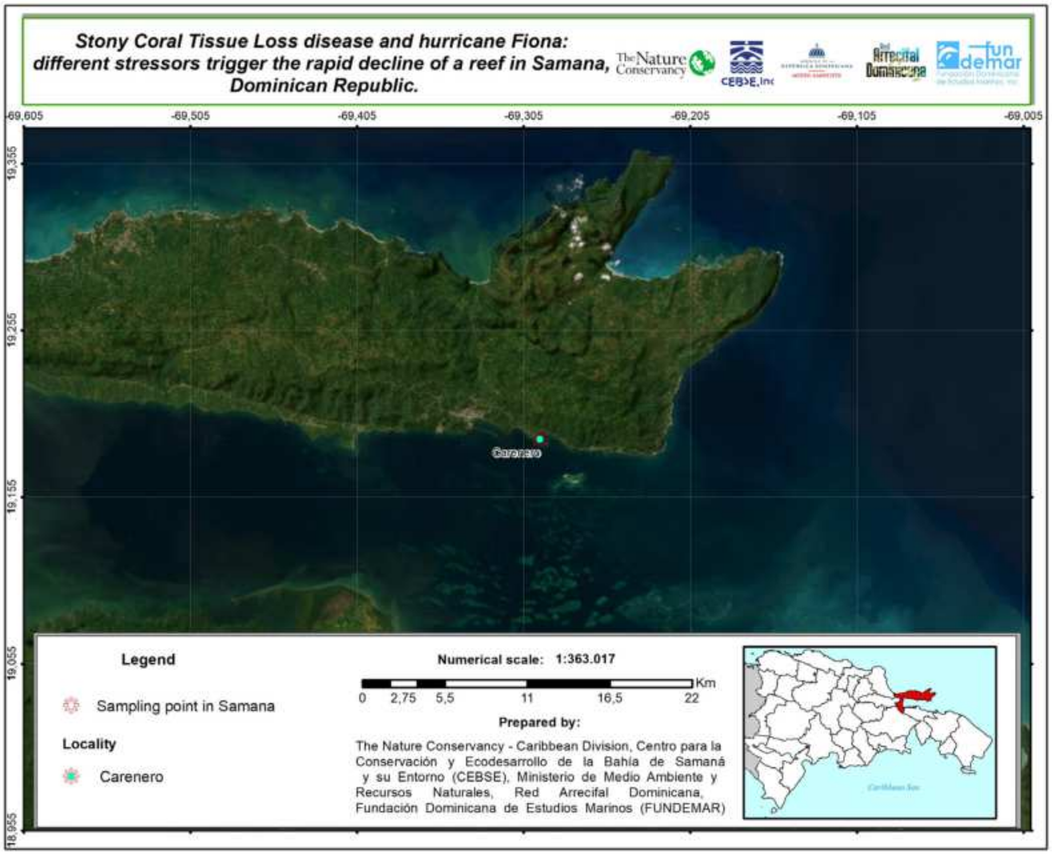

Figure 1. *Geographic location of the monitored reef site at Carenero, Samana Bay, Dominican Republic.*

cm quadrat and assigned 25 random points to identify all scleractinian coral, octocoral, hydrocoral, sponge species, as well as major algal guilds (e.g. turf, macro algae, benthic cyanobacterial mats and calcareous algae) and abiotic substrate (hard and soft). From this analysis, we obtained 2 matrixes to assess benthic coverage of different taxonomic resolutions (i.e., major benthic groups and species level) using the same R code outlined by Miyazawa et al. (2020). Data are presented as mean ± se.

Experimental design and statistical analysis

A 2—factor and fixed orthogonal design was used in order to describe temporal changes in benthic assemblage structure and disease: (1) year with 3 levels (2021, 2022 and 2023) and (2) quarter with 3 levels (first, second and third quarter). For each year, the first quarter extended from February to April, with sampling done in late March and/or mid—April. The second quarter ran from July to September, with sampling conducted between July and early September. Finally, the third quarter spanned from October to December, with sampling conducted between October and late November. We conducted the surveys within a 5—day period each year. Thus, each quarter is set to capture temporal changes on the benthic habitat and on coral disease prevalence within years rather than monthly variability within quarters. The design generated 4 sources of variation: (1) size effect of year, (2) size effect of quarter, (3) fixed interaction between year and quarters and (4) the residual. The strategy for data analysis included 3 steps: (1) visualization of temporal patterns of benthic assemblages and coral disease prevalence, (2) the formal test of no statistical differences for both benthic assemblages and disease prevalence and, (3) the formal test of lack of correlation between temporal changes on disease prevalence and observed temporal trends on benthic assemblages.

For the visualization of benthic assemblages, we used non—metric multidimensional scaling (nMDS) based on Bray—Curtis index (BCI) calculated from a matrix of n = 210 samples (i.e., 10 images x 3 transects x 7 sampling time points) and P variables (benthic categories and/or species depending on taxonomic resolution). In addition, we used a second—stage nMDS plot (Clarke and Gorley 2005) computed from multiple RELATE tests that correlated association matrices (benthic groups or species/genera depending on taxonomic resolution) and then overlay the temporal trajectory of the benthic assemblages recorded for each combination of transect x year x quarter.

For the visualization of temporal patterns of coral disease prevalence, we used a similar approach with the BCI calculated from a matrix of n = 21 samples (i.e., 3 belt—transects x 7 sampling time points) and P variables (i.e., diseases and conditions). We overlaid statistically significant clusters after running a Similarity Profile analysis (SIMPROF) and represented the most relevant variables (diseases and other conditions) explaining the ordination patterns as bubble plots (Clarke and Warwick 2001). Lastly, to visualize potential correlations between temporal changes in benthic assemblages and the occurrence of diseases, we first averaged the benthic matrixes to obtain a 21—row matrix (i.e., n = 21, 3 belt transects x 7 sampling time points). Then, we ran a Principal Coordinate analysis (PCoA, Clarke and Gorley 2005, Anderson et al. 2008) to represent the position of centroids of the benthic assemblages and the variable(s) better correlated (>80%) with the first 2 PCoAs represented as bubbles in a Bray Curtis ordination space.

To test the lack of temporal changes in coral disease prevalence and benthic community structure, we used a Multivariate Permutation Analysis of Variance (PERMANOVA, Anderson 2014) based on BCI as data were not normally distributed but dispersion among groups was uniform (Anderson and Walsh 2013). Post hoc comparisons based on permutations were conducted for significant sources of variation (interactions and/or main effects). In addition, we tested the lack of covariance between temporal changes in benthic assemblages and

2 covariates: (1) disease prevalence and (2) percentage of dead colonies. Finally, we tested the lack of correlation between the benthic and the disease prevalence matrices using a RELATE test (Clarke and Warwick 2001). Then, we ran a BEST test to determine the variables (disease percentage and other conditions) that better explained the correlation between these 2 matrices (Clark and Warwick 2001). From this analysis, a subset of variables was chosen to perform a Distance—based Linear Model (DistLM, Legendre and Anderson 1999, Anderson et al. 2008) to determine the contribution of each variable (i.e., disease prevalence and colony conditions) to the temporal variability of benthic communities. We conducted all analyses with PRIMER + Permanova V7 (Primer—e LTD, Plymouth, Anderson et al. 2008).

Results

Benthic assemblages in Carenero remained relatively stable during 2021, with scleractinian live coral cover ranging from 16.6—19.4% and a mean of 18.31 ± 2.1% (Table 1). Overall, macroalgae dominated the substrate throughout the year (34.04 ± 3.82%); octocorals were consistently present (10.37 ± 1.24%) while the cover of sandy patches averaged 26.79 ± 4.25% and dead hard substrate (e.g. recently dead coral) remained below 5% (mean 2.8 ± 1.2%) (Table 1). In 2021, 19 coral species composed the coral assemblage, with species in the genus *Orbicella* accounting for 6.20% cover (33% relative cover), while *C. natans* (3.12 ± 2.33%), *P. strigosa* (1.8 ± 0.72%), *M. cavernosa* (2.24 ± 0.83%), *Diploria labyrinthiformis* (1.32 ± 0.49%) and *Porites astreoides* (1.02 ± 0.56%) contributed with 52% relative cover (Table 2).

We found a statistically significant interaction between years and quarters for both benthic groups (Pseudo F = 5.53, df = 2, p = 0.001, CV = 17.06) and species (Pseudo F = 5.29, df = 2, p = 0.001, CV = 17.26; Table 3 a—b). Post hoc comparisons for the year x quarter interaction showed statistically significant differences for all years at quarter 1 and between 2021 and 2022 for quarters 2 and 3, this pattern being consistent for both taxonomic resolutions (i.e., benthic groups and species/genera) (Supplementary Table S1).

The nMDS shows evident changes for both taxonomic resolutions (i.e., benthic groups and species/genera), further indicating that benthic assemblages in Carenero rapidly shifted, particularly in 2022 (Figure 2A—C). Major changes leading to coral reef decline through 2022 included: (1) a 3—fold percent reduction (77%) of live coral cover, (2) a 6—fold increase of turf algae cover, (3) a 5—fold increase in benthic cyanobacterial mats (BCMs) and (4) a 12—fold increase of dead coral cover from the mean coverage recorded in 2021. The increased percentage of dead corals (Table 1), matched with the arrival of sctld and extended throughout Q1 and Q2 of 2022. In terms of coral species, we also observed rapid changes (Figure 3A). By the end of 2022, (mean) benthic cover for the 3 *Orbicella* spp. had reduced from 6.2% to less than 1% (15.3% relative cover) whereas *C. natans* and *P. strigosa* had decreased from 1.77% and 3.12% to 0.26% and 0.31%, respectively. Finally, *M. cavernosa* mean coverage was reduced from 2.24% to 0.7% (Table 2, Figure 3B,C). Coral assemblages were correlated throughout the 3 quarters of 2021 and less correlated by the first quarter of 2022; these results further indicate a clear declining trajectory detected for both taxonomic resolutions (Figure 3D).

Similar to benthic assemblages, we found a statistically significant interaction between years and quarters in disease prevalence and other conditions (Table 3C). Post hoc comparisons for the year x quarter interaction showed that health conditions of the colonies in Carenero between years started to change from the second quarter of 2022 (Supplementary Table S1). Diseases such as sctld and CYBD started peaking during the first quarter of 2022 and rapidly expanded throughout the

TABLE 1. *Mean (± sd) cover (%) for major benthic groups recorded in Carenero reef, Dominican Republic in the quarters of 2021, 2022 and 2023. SCTL—scleractinian corals; OCT—octocorals; MILL—Milleporids; TALG—turf algae; MALG—macroalgae; CYAN—benthic cyanobacterial mats; SPON–Sponge; DCALG—dead calcareous algae; DOCT—dead octocorals; DSPON—dead sponge; DCOR—dead scleractinian coral; ABIO–H—abiotic hard bottom (bared substrate); ABIO–S—abiotic sand; OTHR—other benthic organisms.*

Year	Quarter	SCTL	OCT	MILL	TALG	MALG	CYAN	SPON	DCLAG	DOCT	DSPON	DCOR	ABIO-H	ABIO-S	OTHR
2021															
	1	18.93	9.52	1.66	5.24	30.52	1.10	4.94	0.14	0.69	0.90	0.00	4.00	21.66	0.71
	2	19.40	9.80	2.80	0.40	33.60	0.40	0.60	0.00	1.00	0.60	0.00	1.60	29.60	0.20
	3	16.60	11.80	1.70	0.50	26.00	0.90	2.70	0.10	2.30	0.10	1.50	2.80	29.10	3.90
	Mean	**18.31**	**10.37**	**2.05**	**2.05**	**30.04**	**0.80**	**2.75**	**0.08**	**1.33**	**0.53**	**0.50**	**2.80**	**26.79**	**1.60**
	sd	**1.50**	**1.24**	**0.65**	**2.77**	**3.82**	**0.36**	**2.17**	**0.07**	**0.85**	**0.40**	**0.87**	**1.20**	**4.45**	**2.01**
2022															
	1	7.20	8.00	7.87	6.13	28.80	0.53	3.60	1.20	1.07	0.40	2.93	2.00	30.13	0.00
	2	6.13	10.67	2.53	8.53	25.00	10.53	1.47	0.00	2.13	0.13	8.73	3.60	20.13	0.27
	3	4.77	7.74	1.42	26.45	8.13	1.03	1.03	1.42	0.52	0.77	6.84	6.32	33.29	0.26
	Mean	**6.02**	**8.79**	**3.91**	**13.85**	**20.51**	**4.00**	**2.02**	**0.88**	**1.23**	**0.44**	**6.18**	**4.00**	**27.91**	**0.18**
	sd	**1.22**	**1.62**	**3.45**	**11.10**	**11.00**	**5.64**	**1.37**	**0.76**	**0.82**	**0.32**	**2.96**	**2.19**	**6.87**	**0.15**
2023															
	1	5.47	12.80	0.80	21.73	3.07	0.80	1.87	1.33	1.33	0.00	4.80	8.80	37.20	0.00

TABLE 2. *Mean (± sd) cover (%) for 19 coral species found in Carenero reef site, Dominican Republic, in quarters of 2021, 2022 and 2023. Following AGRRA's nomenclature (www.agrra.org), columns are coral species, the first capital letter corresponding to the genus and the 3 consecutive lower-case letters corresponding to the species. SCL–scleractinian coral.*

Year	Quarter	Oann	Ofra	Ofav	Pstr	Dlab	Cnat	Mcav	Past	Ppor	Pdiv	Ssid	Aaga	Alam	Efast	Sbou	Dsto	Afra	Lcuc	Srad	Total SCL
2021																					
	1	2.43	0.14	4.14	1.12	1.86	1.97	1.83	1.65	0.14	0.00	3.10	0.14	0.00	0.00	0.00	0.00	0.14	0.28	0.00	18.93
	2	2.60	0.00	1.60	1.80	1.20	5.80	3.20	0.60	0.20	0.00	2.00	0.20	0.00	0.20	0.00	0.00	0.00	0.00	0.00	19.40
	3	2.30	0.70	4.70	2.40	0.90	1.60	1.70	0.80	0.30	0.00	0.40	0.20	0.00	0.40	0.00	0.10	0.00	0.10	0.00	16.60
	Mean	**2.44**	**0.28**	**3.48**	**1.77**	**1.32**	**3.12**	**2.24**	**1.02**	**0.21**	**0.00**	**1.83**	**0.18**	**0.00**	**0.20**	**0.00**	**0.03**	**0.05**	**0.13**	**0.00**	**18.31**
	sd	**0.15**	**0.37**	**1.65**	**0.64**	**0.49**	**2.33**	**0.83**	**0.56**	**0.08**	**0.00**	**1.36**	**0.04**	**0.00**	**0.20**	**0.00**	**0.06**	**0.08**	**0.14**	**0.00**	**1.50**
2022																					
	1	0.27	0.00	0.13	0.27	0.27	0.27	1.07	1.33	0.53	0.13	1.73	0.27	0.27	0.13	0.00	0.00	0.27	0.27	0.00	7.20
	2	0.67	0.00	1.73	0.13	1.20	0.27	0.27	0.40	0.53	0.00	0.53	0.13	0.00	0.00	0.27	0.00	0.00	0.00	0.00	6.13
	3	0.00	0.00	0.00	0.39	0.00	0.39	0.77	0.13	0.13	0.00	0.65	0.00	0.65	0.00	0.00	0.13	1.42	0.00	0.13	4.77
	Mean	**0.31**	**0.00**	**0.62**	**0.26**	**0.48**	**0.31**	**0.70**	**0.62**	**0.40**	**0.04**	**0.97**	**0.13**	**0.31**	**0.04**	**0.09**	**0.04**	**0.57**	**0.09**	**0.04**	**6.02**
	sd	**0.34**	**0.00**	**0.96**	**0.13**	**0.63**	**0.07**	**0.40**	**0.63**	**0.23**	**0.08**	**0.66**	**0.13**	**0.32**	**0.08**	**0.15**	**0.07**	**0.75**	**0.15**	**0.07**	**1.22**
2023																					
	1	**0.67**	**0.00**	**0.80**	**0.00**	**0.00**	**0.00**	**0.67**	**0.40**	**0.00**	**0.13**	**0.53**	**0.13**	**0.40**	**0.00**	**0.13**	**0.00**	**1.20**	**0.40**	**0.00**	**5.47**

TABLE 3. *Two-way Permutational Multivariate Analysis of Variance (PERMANOVA) on the Bray-Curtis index of resemblance for corals and benthos at the Carenero reef site, Dominican Republic. A. Major benthic groups. B. Major species/genera. C. Coral diseases and other conditions. Statistically significant if p < 0.05. Ye–Year; Qu–quarter; Res–Residuals; perm refers to the permutations used to generate statistical results; CV—coefficient of variation. ** Denotes there are empty cells for the source of variation.*

Source	df	SS	MS	Pseudo-F	P(perm)	perms	CV
			A. Major Benthic Groups				
Ye	2	49,117	24558.0	24.9	0.001	999	27.1
Qu	2	13,634	6817.1	6.9	0.001	998	13.5
Ye x Qu**	2	11,316	5657.9	5.7	0.001	999	17.05
Res	203	200,410	987.3				42.3
Total	209	270,230					
			B. Major species/genera				
Ye	2	62321	31161	18.5	0.001	999	24.6
Qu	2	20168	10084	5.9	0.001	998	13.1
Ye x Qu**	2	17873	8936.3	5.3	0.001	999	17.3
Res	203	342900	1689.2				44.9
Total	209	436870					
			C. Prevalence of coral diseases and other conditions				
Ye	2	1097.8	548.9	3.4	0.006	999	18.1
Qu	2	810.9	405.5	2.5	0.023	999	32.4
Ye x Qu**	2	1183.2	591.6	3.6	0.017	999	49.5
Res	14	2272.4	162.3				
Total	20	5590.2					

reef during the second and third quarters of that year (Table 4; Figure 4A—H). Furthermore, the permutational multivariate analysis of covariance showed that loss of coral cover significantly covariates with the rise of sctld prevalence and the concomitant increase in number of dead colonies recorded for the species listed above (Table 5, Figure 5A—D). The DistLM analysis showed that the total disease and CYBD prevalence and the percentage of dead colonies explained about 35% of the temporal variability of major benthic groups recorded from 2021 to the first quarter of 2023; however, only the percentage of dead colonies was statistically significant (Table 6).

Other important events recorded and potentially driving the observed shifts of sessile benthic communities in Carenero were the observed increased sedimentation and arrival of BCMs (second quarter of 2022) that were previously not noted; this observation coincided with the arrival of Hurricane Fiona during the last quarter of 2022. Sediment smoothed small and large coral species and BCMs often overgrew coral surfaces, producing lesions on larger reef building species (Supplemental Figure S1C). As a presumed consequence, the percentage of cover of dead scleractinian corals increased in 2022 compared to all quarters surveyed in 2021. Lastly, when hurricane Fiona came though during the last quarter of 2022, large colonies formerly affected by sctld and CYBD were observed detached from the substrate and tilted (Figure 4J—K). In shallower habitats of Carenero, the hurricane destroyed a large thicket of *A. cervicornis* that had remained healthy for years (Supplementary Figure S1A—B). Additionally, the 2023 Caribbean bleaching event affected the remaining populations of corals (Supplementary Figure S1D—E).

Discussion

In this paper, we showed that sctld and CYBD combined with other stressors such as hurricanes, sedimentation, and me-

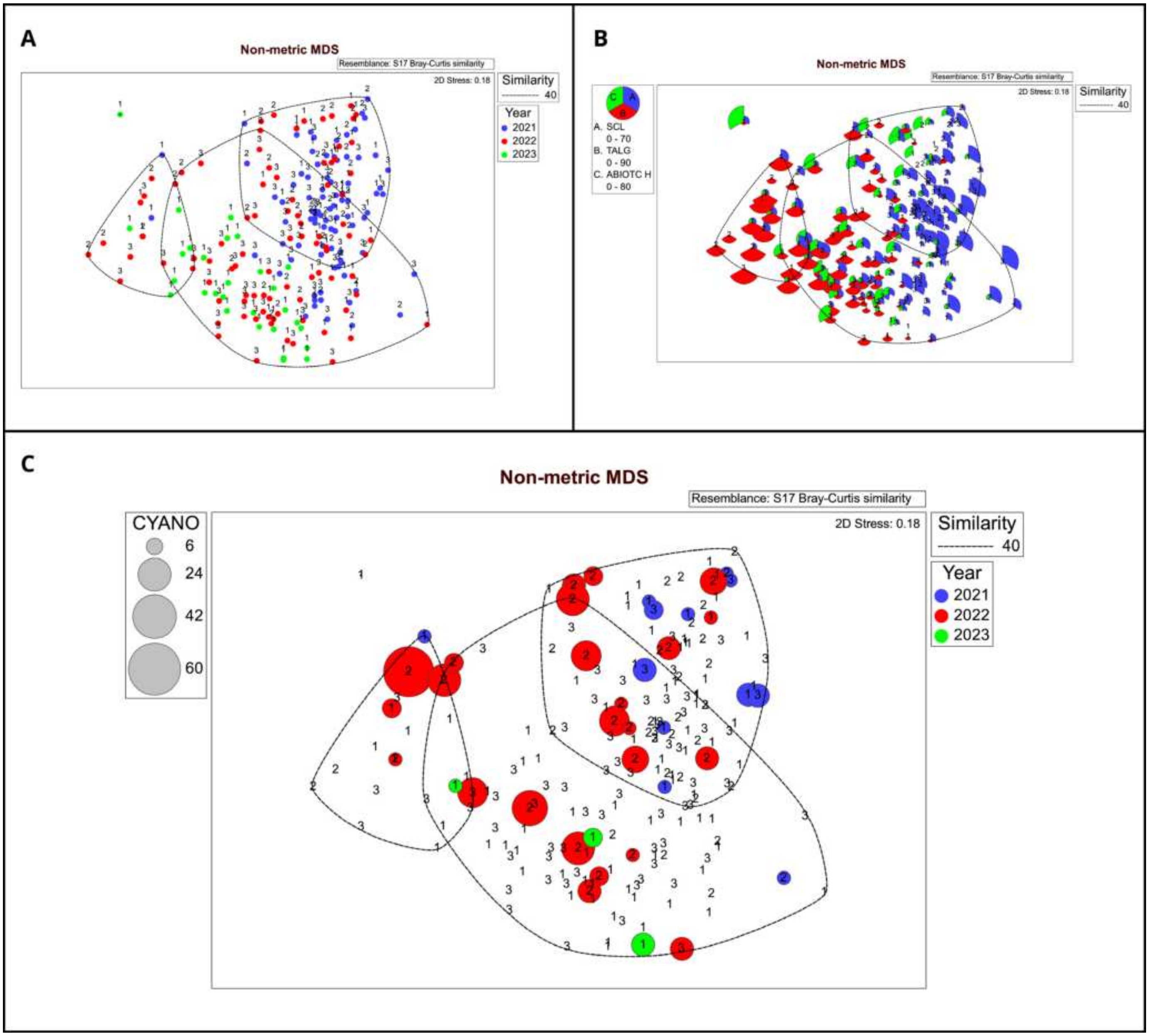

Figure 2. *nMDS showing ordination of benthic samples from Carenero, Samana Bay, Dominican Republic in a Bray Curtis space for each quarter of 2021, 2022 and the first quarter of 2023. A. Major benthic groups. B. Bubble plots showing percentage cover for major benthic groups. C. Bubble plots showing percentage cover for benthic cyanobacterial mats. Clusters represent 40% of similarity. Dots represent samples (based on photos) and numbers the quarters for each year (blue dots – 2021; red dots — 2022; green dots — first quarter of 2023). SCL — scleractinian corals; TALG — turf algae; ABIOH — abiotic hard bottom (bared substrate + dead coral); CYANO — benthic cyanobacterial mats.*

chanical abrasion, triggered rapid changes within a few months. In 2021, mean live coral cover in Carenero was 18.31% ± 1.5, but experienced a sudden decline as the benthic assemblage shifted. According to national surveys published by ReefCheck in 2023, reefs with higher live coral cover seldom reached averages above 20% (Steneck and Torres 2023). Thus, in 2021, Carenero was perhaps amongst the best coral reefs for the Dominican Republic context. Our results show that benthic assemblages in Carenero lost about 77% of live coral cover between the last quarter of 2021 and the first quarter of 2022. By the first quarter of 2023, almost 80% of that cover had been already lost. Rapid loss of live coral cover was a consequence of 16—100% mortality recorded for 6 coral species (i.e., *C. natans*, *M. cavernosa*, *P. strigosa*, *O. faveolata*, *O. annularis* and *O. franksi*) through the first half of 2022. These results highlight the value of permanent monitoring programs and frequent coral reef surveys to assess and assign the role of various stressors and drivers of rapid change. The identification of these stressors demands the design of contingency plans to tackle the problem of coral disease epizootic events, and highlights the importance of rapid action to control the problems of coastal development in Samana as well as designing mitigation plans to reduce the impact

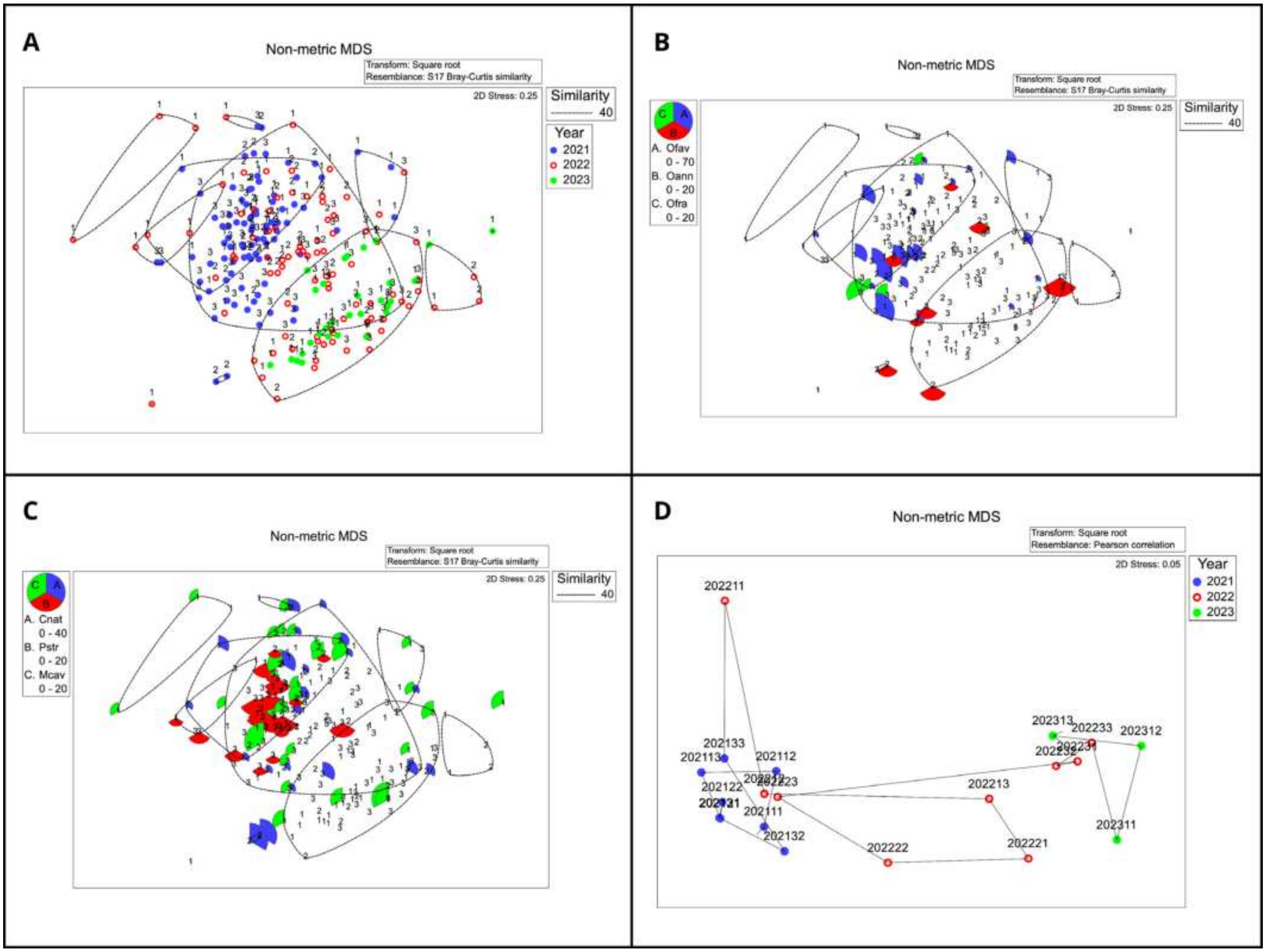

Figure 3. *nMDS showing ordination of coral samples from Carenero, Samana Bay, Dominican Republic in a Bray Curtis space for each quarter of 2021, 2022 and the first quarter of 2023. A. Major coral species. B. Relative cover percentage per species for* Orbicella faveolata *(Ofav),* O. annularis *(Oann) and* O. franksi *(Ofra). C. Relative cover percentage per species for* Colpophyllia natans *(Cnat),* Pseudodiploria strigosa *(Pstr), and* Montastraea cavernosa *(Mcav). Clusters represent 40% of similarity. Dots represent samples (quadrats) and numbers the quarters for each year. D. Temporal trajectory (arrowed line) of scleractinian coral assemblages displayed in a Spearman correlation ordination space. Each dot represents the centroid of year (first 4 digits), transect (fifth digit) in a quarter (last digit). The closer the dots, the more correlated is the coral assemblage.*

of sedimentation.

Permanent monitoring allowed us to establish a precise chronology of events that led to rapid shits of the benthic assemblages of Carenero. Early in 2021, Croquer et al. (2022a) reported an ongoing sctld epizootic event in Samana; however, we observed no colonies bearing sctld macroscopic signs in Carenero until the last quarter of that year. During the first quarter of 2022, cases of sctld started to appear with prevalence that seldom exceeded 6% in the coral community. The low prevalence of sctld recorded in Carenero compared to other sites of Samana and Galeras (see Croquer et al. 2022a) is explained by the predominance (in terms of number of colonies) of species that are less susceptible to sctld (e.g. *Porites* spp, *Agaricia* spp. *Stephanochoenia intersepta*, etc.), a pattern also observed by Gintert et al (2019). During the second quarter of 2022, the prevalence of sctld remained below 6%; however, the percentage of recently dead colonies rapidly increased 4–fold from 2021 to 2022. In addition, during this period, the prevalence of CYBD peaked, reaching values above 60% for the 3 species in the genus *Orbicella* spp. Thus, our study shows that even at low prevalence in the coral community, diseases can reduce live coral cover drastically in reefs where few large colonies of major reef–building coral species provide the bulk of live coral cover, while smaller and less susceptible species remain healthy and/or with lower mortality.

Our findings support the conclusion that coral diseases in the Caribbean continue to have a primary role in the rapid degradation of reefs across the region as previously reported (Weil 2004). Impacts of epizootic events of white band disease (WBD), white plague type I and II (WPD–I, II), CYBD and,

TABLE 4. *Mean (± sd) prevalence (%) of coral diseases and other conditions recorded at Carenero reef site, Dominican Republic, in the quarters of 2021, 2022 and 2023. Significance if p < 0.05. Suspected diseases based on visualization include BBD–black band disease; WPD–white plague disease; sctld–Stony Coral Tissue Loss Disease; CYBD–Caribbean Yellow band disease; DSD–Dark Spot Disease. Other–unidentified macroscopic disease signs.*

Year	Quarter	Healthy	Diseased	BBD	WPD	SCTLD	CYBD	DSD	Pale	Bleached	Other	Predation
2021												
	1	98.35	0.20	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	1.45
	2	96.95	1.07	0.00	0.00	1.07	0.00	0.00	0.77	0.00	0.00	1.20
	3	77.91	18.41	1.62	0.00	0.00	0.00	16.64	0.00	3.31	0.16	0.37
	Mean	**91.07**	**6.56**	**0.54**	**0.00**	**0.36**	**0.00**	**5.61**	**0.26**	**1.10**	**0.05**	**1.01**
	sd	**11.42**	**10.27**	**0.93**	**0.00**	**0.62**	**0.00**	**9.55**	**0.45**	**1.91**	**0.09**	**0.57**
2022												
	1	94.03	3.32	0.00	0.00	3.07	0.00	26.00	2.39	0.00	0.00	0.26
	2	88.48	6.65	0.00	0.28	2.14	3.46	0.76	2.71	1.05	0.00	1.11
	3	97.66	0.39	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00	1.95
	Mean	**93.39**	**3.45**	**0.00**	**0.09**	**1.74**	**1.15**	**0.47**	**1.70**	**0.35**	**0.00**	**1.11**
	sd	**4.62**	**3.13**	**0.00**	**0.16**	**1.57**	**2.00**	**0.26**	**1.48**	**0.60**	**0.00**	**0.85**
2023												
	1											
	Mean	**96.56**	**1.42**	**0.00**	**0.00**	**0.18**	**0.36**	**0.88**	**1.09**	**0.09**	**0.00**	**0.84**
	sd	**3.01**	**2.25**	**0.00**	**0.00**	**0.31**	**0.62**	**1.32**	**1.26**	**0.15**	**0.00**	**1.02**

more recently, sctld are undisputable. White band disease wiped out populations of Caribbean acroporids (*Acropora palmata* and *A. cervicornis*) across the region (Aronson and Precht 2001, Weil et al. 2006, Sokolow 2009, Weil and Rogers 2010), and 40 years after the massive mortality, it is still unclear if these species will recover throughout their original distributional range (Croquer et al. 2016, Martinez et al. 2021). Both WPD type II and I where the first epizootic events targeting and reducing population numbers of multispecies hosts, becoming highly prevalent in the earlier 1970's for more than 45 years (Bruckner 2015 Croquer et al. 2021). White diseases spread out fast from Bermuda (Weil and Croquer 2009, Croquer and Weil 2009a) and Florida (Richardson and Voss 2005) to Venezuela (Croquer et al. 2003), the Lesser Antilles (Weil and Croquer 2009, Croquer and Weil 2009a), Puerto Rico (Weil et al. 2009b), Colombia (Navas–Camacho et al. 2010) and the Mexican Caribbean (Randazzo–Eisemann et al. 2021). In several cases, WPD–II epizootic events led to a rapid loss of live coral cover, particularly after the 2005 and 2010 massive bleaching events (Miller

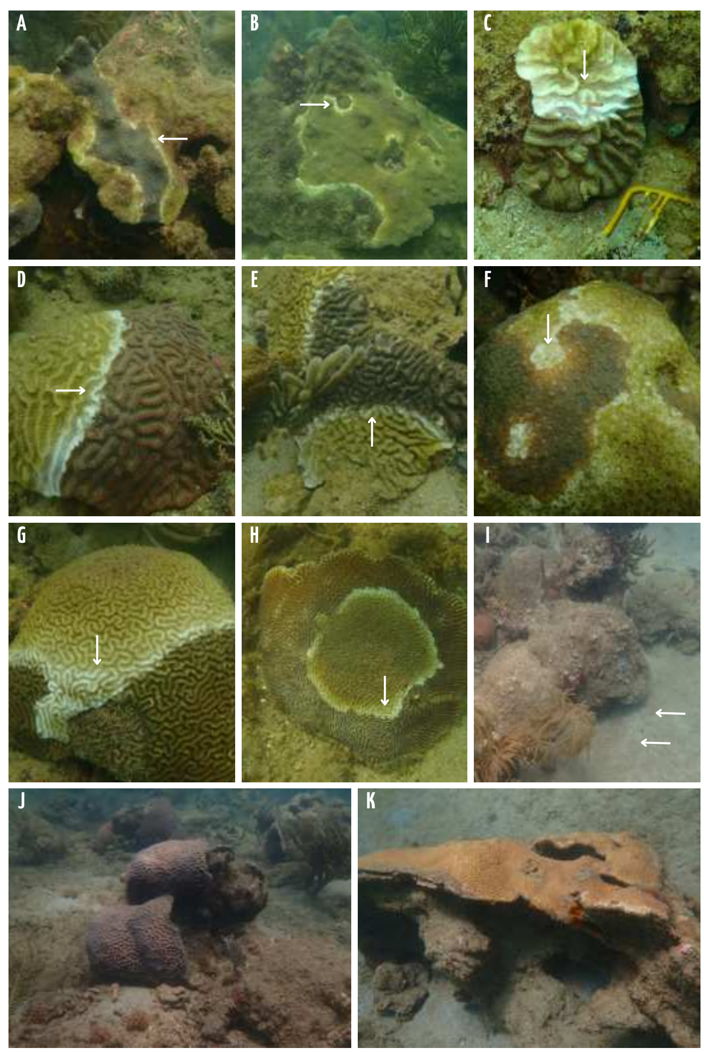

Figure 4. *Photographic record of coral diseases and other stressors observed in Carenero, Dominican Republic from 2021 to the first quarter of 2022. A.* Orbicella faveolata *showing macroscopic signs of stony coral tissue loss disease (sctld, arrow). B.* O. faveolata *showing macroscopic signs of Carribean Yellow Band Disease (CYBD, arrow). C–E. Different colonies of* Colpophyllia natans *showing macroscopic signs of sctld (arrow). F.* Montastraea cavernosa *showing sctld macroscopic signs (arrow). G–H.* Pesudodiploria strigosa *colonies showing macroscopic signs of sctld (arrow). I. Colonies smoothed by sediments. White arrows indicate silty sediments deposited in the substrate after rains recorded in April 2022. J. Tilted colonies of* M. cavernosa. *K.* O. faveolata *detached and lifted after Hurricane Fiona.*

TABLE 5. *Permutational Multivariate Analysis of Variance (PERMANOVA) with 3 covariates included (Total prevalence sctld, CYBD and DEAD prevalence) and percentage of dead colonies to explain changes in benthic cover at Carenero reef site, Dominican Republic, from 2021 and 2023. Significant if p < 0.05. perm refers to the permutations used to generate statistical results; CV—coefficient of variation.** Denotes there are empty cells for the source of variation.*

Source	df	SS	MS	Pseudo-F	P(perm)	perms	CV
Total SCTLD	1	1216.5	1216.5	4.6334	0.003	999	7.98
Total CYBD	1	397.51	397.51	1.514	0.231	999	3.22
Total DEAD	1	2110.6	2110.6	8.0387	0.001	998	11.12
Ye	2	4383.5	2191.7	8.3478	0.001	999	23.55
Qu	2	1761.6	880.78	3.3547	0.009	999	15.65
YexQu**	2	1583.4	791.72	3.0155	0.005	999	19.28
Res	11	2888.1	262.55				19.19
Total	20	14341					

et al. 2009, Croquer and Weil 2009b, Eakin et al. 2010). Furthermore, since first noticed, CYBD has also produced significant impacts on populations of *Orbicella* spp. over the past 3 decades, reducing population numbers in countries such as Puerto Rico (Bruckner and Bruckner 2006) and compromising the reproductive output of *O. faveolata* (Weil et al. 2009a). In this, paper we correlate the rapid shift of coral assemblages with the arrival of sctld and CYBD, 2 diseases that had a clear role by affecting major reef builders in the study site.

More recently, sctld has produced the largest and perhaps the worst long—lasting impacts on Caribbean coral reefs as it has significantly reduced populations of corals that survived former epizootic events recorded during the 1970's, 1980's and late 1990's. According to the ICUN coral specialist group, sctld has become the primary threat for the vast majority of Western—Atlantic corals (IUCN Species Red List assessment 2023). Species in the genus *Colpophyllia*, *Pseudo-*

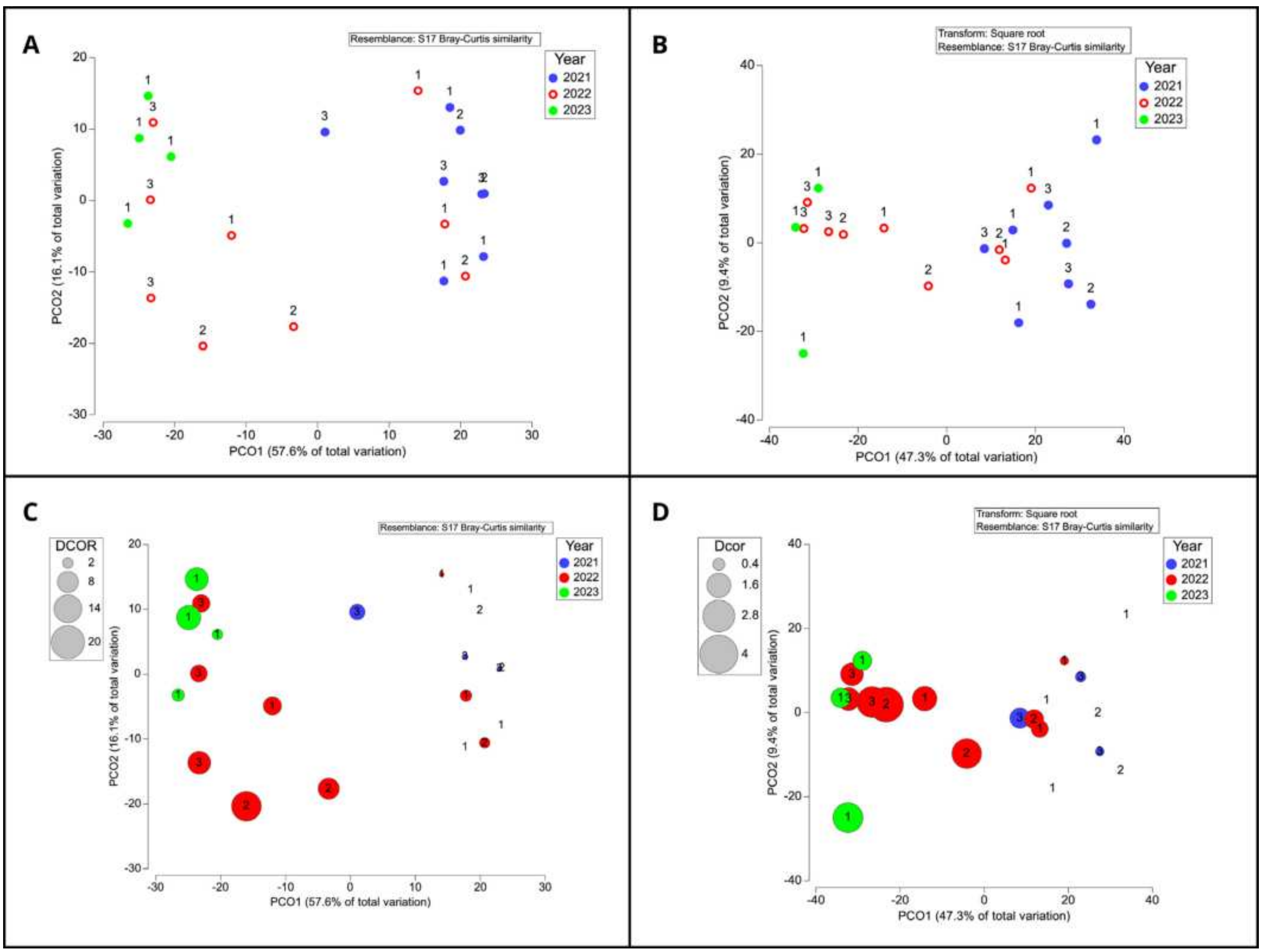

Figure 5. *Principal coordinate analysis (PCoA) showing the position of transects and quarters for each of the years (2021, 2022 and 2023) monitored at Carenero, Samana Bay, Dominican Republic. A. Temporal changes for major benthic groups. B. Temporal changes for species/genera. C. Percentage of Dead Coral Colonies (DCOR) recorded for each transect, quarter and monitoring year plot in the PCoA computed from major benthic group Bray—Curtis association matrices. D. Percentage of Dead Coral Colonies (DCOR) recorded for each transect, quarter and monitoring year plot in the PCoA computed from the coral species Bray—Curtis association matrices.*

TABLE 6. *Distance-based Linear Model from a Bray-Curtis similarity index (major taxonomic groups as response variables) and prevalence (%) of diseases and other conditions as predictors. SCTLD—stony coral tissue loss disease; CYBD—Caribbean yellow band disease; DSD—Dark spot disease; Total DC—total dead colonies. Significant at p < 0.05.*

Variable	SS(trace)	Pseudo-F	p	Prop.
Total SCTLD	484.98	0.3676	0.726	0.0189
Total CYBD	2673.4	2.2201	0.113	0.1046
Total DSD	1909.2	1.5343	0.257	0.0747
Total Pale	100.16	0.074768	0.972	0.0039
Total Bleached	1631.1	1.2956	0.272	0.0638
Total diseased	1400.1	1.1014	0.36	0.0547
Total DC	5008.8	4.6326	0.005	0.1960

diploria, *Orbicella* and *E. fastigiata* that represented little to no concern of extinction in 2000, are now vulnerable, endangered, or critically endangered (Croquer et al. 2022c). Furthermore, sctld has driven populations of *D. cylindrus*, *Meandrina meandrites* and *E. fastigiata* to virtual local extinction in the Mexican Caribbean (Alvarez—Filip et al. 2022), the Florida Keys (Neely et al. 2021) and in other areas of the Caribbean (Brandt et al. 2021, Croquer et al. 2021. Other significant impacts of sctld on Caribbean coral assemblages include loss of biodiversity and structural complexity and replacement of species composition (Alvarez—Filip et al. 2022). In the Dominican Republic, sctld was first noticed in Cayo Arena (Irazabal and Rodríguez 2019) and has since spread out fast northwest (Punta Rucia to Sousua), northeast (Terrenas, Galeras and Samana), east (Bavaro to Cap Cana), southeast (Bayahibe) and southwest (Pedernales) from 2019 to 2023 (Croquer et al. 2022a, Villalpando et al. 2022, Steneck and Torres 2023). In the Dominican Republic, highly susceptible coral families (e.g. Meandrinidae), genera and species to sctld are consistent with the ones reported across the Caribbean region. However, there are areas such as Caleta and Boca Chica where sctld has not arrived yet (Steneck and Torres 2023). While no studies have formally assessed the impact of sctld in the Dominican Republic throughout its whole distribution range, devastating mortality has been reported (Croquer et al. 2022a, Villalpando et al. 2022). Furthermore, Steneck and Torres (2023) pointed out that sctld, together with other diseases, were major drivers of change in coral reefs. Thus, this is the first quantitative multivariate study to estimate the actual impact of sctld on a Dominican coral reef.

The rise of mortality in Carenero also coincided with an increase in benthic cover of silty sediments between 9—11 m that we started recording after the arrival of Hurricane Fiona during the last quarter of 2022. Increased cover of silty sediments coincided with 2 events that occurred during the second quarter of 2022: (1) the initiation of construction of a pier located a few kilometers away from the bay and (2) runoff following rain storms. Sedimentation is one of the primary stressors affecting coral reef health at local scales and because of the rapid coastal development that Caribbean islands are experiencing with the rise of tourism, sedimentation has become a regional problem. The direct and/or indirect effects of acute and chronic inputs of sedimentation are well understood since the 1990's (Rogers 1990), and recently reviewed by Rogers and Ramos—Scharrón (2022). Indirectly, sediments and terrestrial runoff change water quality and hampers penetration of light for corals depending on how long sediments remain suspended in the water column (Rogers and Ramos—Scharrón 2022). Directly, sediments can smooth corals, suffocating colonies and increasing respiration and photosynthesis rates and mucus production, further affecting the energetic budget of corals (Rogers and Ramos—Scharrón 2022). Secondary infections may produce rapid mortality of tissues if sediments are deposited for long periods and mixed with coral mucus (Weber et al. 2012). Various studies have shown a positive correlation between the occurrence of Black Band Disease (BBD), terrestrial runoff and sedimentation (Kuta and Richardson 2002, Voss and Richardson 2006). Recent surveys conducted in August 2024 confirm that sedimentation still represents a threat in Carenero as silty sediments have buried entire colonies in deeper sections of the reef.

Another problem detected in Carenero during the second quarter of 2022 was a bloom of benthic cyanobacterial mats. Whilst BCMs can bloom seasonally at some locations, their prevalence and duration are increasing at an alarming rate (de Bakker et al. 2017, Ford et al. 2018). The factors directly responsible for these changes remain uncertain but decreasing water quality and increasing water temperatures seem to be the underlying causes behind these blooms (Ford et al. 2018). Our data suggest that BCMs in Carenero are an increasing problem, with cover seldom exceeding 4% in 2021 but rising 3—fold during March—April 2022. In other Caribbean countries such as Curacao, long—term monitoring programs have shown that BCMs are becoming a permanent feature of Caribbean reefs (de Bakker et al. 2017, Ford et al. 2018). Furthermore, recent studies show that BCMs deter herbivory (Cissell et al. 2019) and act as vectors and reservoirs of BBD (Cissell et al 2022). Only through long—monitoring efforts will it be possible to determine if BCMs will become a stable feature of the benthic communities in Carenero and other reefs of the Dominican Republic.

Lastly, during the last quarter of 2022, Hurricane Fiona affected the eastern coast of the Dominican Republic with maximum wind speeds of 150 km/h. Fiona landed at Boca de Yuma and moved northeast while weakening slightly over land. However, after emerging off the northern coast of the Dominican Republic and back over the Atlantic Ocean, it began to intensify again, reaching Category 2 intensity (NOAA Hurricane Center). Our monitoring program recorded the impacts of Hurricane Fiona on benthic and coral assemblages as we observed large colonies of *O. faveolata*, *O. annularis*, *O. franksi* and *C. natans* detached from the substrate and flipped upside down. Furthermore, when Hurricane Fiona landed in Samana, it destroyed one of the healthiest *A. cervicornis* thickets located in shallow habitats of Carenero in a few days.

In conclusion, we show clear evidence of rapid changes, over just a few months, in benthic community assemblages. Only with permanent and frequent monitoring did we manage to follow the chronology of a series of stressors that reduced coral cover by half in <6 months. We clearly demonstrated the value of monitoring different indicators to describe the temporal trajectories of benthic and coral assemblages. While coral diseases, mechanical damages and abrasion correlated with the observed short–term declining trend in live coral cover, we cannot disregard the role of other stressors and environmental factors not quantified in this study. We demonstrate the value of monitoring different indicators to describe the temporal trajectories of benthic and coral assemblages. Furthermore, we portray a case in which sctld prevalence in the coral community could be as low as 3–6% and yet rapidly reduce coral cover when the disease affects large colonies and multiple reef–building coral species. Finally, our results indicate that local environmental authorities must regulate factors that might be contributing to increased terrestrial runoff and sedimentation in Samana Bay to prevent and/or ameliorate further damage to coral reef ecosystems. In the short term, our monitoring program in Carenero and other reefs along the northern coast of the Dominican Republic will assess the impact of the 2023 Caribbean bleaching event that affected the remaining populations of corals.

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Literature Cited

Alvarez–Filip, L., N. Estrada–Saldívar, E. Pérez–Cervantes, A. Molina–Hernández, and F.J. González–Barrios. 2019. A rapid spread of the stony coral tissue loss disease outbreak in the Mexican Caribbean. PeerJ 7:e8069. https://doi.org/10.7717/peerj.8069

Alvarez–Filip, L., F.J. González–Barrios, E. Pérez–Cervantes, A. Molina–Hernández, and N. Estrada–Saldívar. 2022. Stony coral tissue loss disease decimated Caribbean coral populations and reshaped reef functionality. Communications Biology 5:440. https://doi.org/10.1038/s42003–022–03398–6

Anderson, M.J. 2014. Permutational multivariate analysis of variance (PERMANOVA). Wiley statsref: Statistics reference online, p. 1–15. https://doi.org/10.1002/9781118445112.stat07841

Anderson, M.J. and D.C. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs 83:557–574. https://doi.org/10.1890/12–2010.1

Anderson, M.J., R.N. Gorley, and K.R. Clarke. 2008. PERMANOVA + for PRIMER: guide to software and statistical methods. Plymouth: PRIMER–E. https://learninghub.primer–e.com/books/permanova–for–primer–guide–to–software–and–statistical–methods. (viewed on 10/05/2023)

Aronson, R.B. and W.F. Precht. 2001. White–band disease and the changing face of Caribbean coral reefs. In: J.W. Porter, ed. The Ecology and Etiology of Newly Emerging Marine Diseases. Developments in Hydrobiology, vol 159. Springer, Dordrecht, The Netherlands, p. 25–38. https://doi.org/10.1007/978–94–017–3284–0_2

Brandt, M.E., R.S. Ennis, S.S. Meiling, J. Townsend, K. Cobleigh, A. Glahn, and T.B. Smith. 2021. The emergence and initial impact of stony coral tissue loss disease (SCTLD) in the United States Virgin Islands. Frontiers in Marine Science 8:715329. https://doi.org/10.3389/fmars.2021.715329

Bruckner, A.W. 2015. White syndromes of Western Atlantic reef–building corals. In: C.M. Woodley, C.A. Downs, A.W. Bruckner, J.W. Porter, and S.B. Galloway, eds. Diseases of Coral, Chapter 22. Wiley & Sons, Hoboken, NJ, USA, p. 316–332. https://doi.org/10.1002/9781118828502.ch22

Bruckner, A.W. and R.J. Bruckner. 2006. Consequences of yellow band disease (YBD) on *Montastraea annularis* (species complex) populations on remote reefs off Mona Island, Puerto Rico. Diseases of Aquatic Organisms 69:67–73. https://doi.org/10.3354/dao069067

Bruckner, A.W. and B. Riegl. 2015 Yellow–Band Diseases. In: C.M. Woodley, C.A. Downs, A.W. Bruckner, J.W. Porter, and S.B. Galloway, eds. Diseases of Coral, Chapter 27. Wiley & Sons, Hoboken, NJ, USA, p. 376–386. https://doi.org/10.1002/9781118828502.ch27

Carpenter, K.E., M. Abrar, G. Aeby, R.B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortés, J.C. Delbeek, L. DeVantier, G.J. Edgar, A.J. Edwards, D. Fenner, H.M. Guzmán, B.W. Hoeksema, G. Hodgson, O. Johan, W.Y. Licuanan, S.R. Livingstone, E.R. Lovell, J.A. Moore, D.O. Obura, D. Ochavillo, B.A. Polidoro, W.F. Precht, M.C. Quibilan, C. Reboton, Z.T. Richards, A.D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. Veron, C. Wallace, E. Weil, and E. Wood. 2008. One–third of reef–building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563. https://doi.org/10.1126/science.1159196

Cissell, E.C., J.C. Manning, and S.J. McCoy. 2019. Consumption of benthic cyanobacterial mats on a Caribbean coral reef. Scientific Reports 9:12693. https://doi.org/10.1038/s41598–019–49126–9

Cissell, E.C., C.E. Eckrich, and S.J. McCoy. 2022. Cyanobacterial mats as benthic reservoirs and vectors for coral black band disease pathogens. Ecological Applications 32(6):e2692. https://doi.org/10.1002/eap.2692

Clarke, K.R. and R.N. Gorley. 2005. PRIMER: Getting started with v6. PRIMER–E Ltd: Plymouth, UK, 932 p.

Clarke, K.R. and R.M. Warwick. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. 2nd Edition, PRIMER–E, Ltd., Plymouth Marine Laboratory, Plymouth, U.K.

Croquer, A. and E. Weil. 2009a. Changes in Caribbean coral disease prevalence after the 2005 bleaching event. Diseases of Aquatic Organisms 87:33–43. https://doi.org/10.3354/dao02164

Croquer, A. and E. Weil. 2009b. Spatial variability in distribution and prevalence of Caribbean scleractinian coral and octocoral diseases. II. Genera–level analysis. Diseases of Aquatic Organisms 83:209–222. https://doi.org/10.3354/dao02012

Croquer, A., S.M. Pauls, and A.L. Zubillaga. 2003. White plague disease outbreak in a coral reef at Los Roques National Park, Venezuela. Revista de Biologia Tropical 51(4):39–45.

Croquer, A., F. Cavada–Blanco, A.L. Zubillaga, E.A. Agudo–Adriani, and M. Sweet. 2016. Is *Acropora palmata* recovering? A case study in Los Roques National Park, Venezuela. PeerJ 4:e1539. https://doi.org/10.7717/peerj.1539

Cróquer, A., E. Weil, and C.S. Rogers. 2021. Similarities and differences between two deadly Caribbean coral diseases: White plague and stony coral tissue loss disease. Frontiers in Marine Science 8:709544. https://doi.org/10.3389/fmars.2021.709544

Croquer, A., S. Zambrano, S. King, A. Reyes, R. Sellares–Blanco, A. Valdez Trinidad, and E. Miyazawa. 2022a. Stony coral tissue loss disease and other diseases affect adults and recruits of major reef builders at different spatial scales in the Dominican Republic. Gulf and Caribbean Research 33:GCFI1–GCFI13. https://doi.org/10.18785/gcr.3301.03

Croquer, A., S. Zambrano, I. Irazabal and R. Torres. 2022b. Factores globales y locales que inciden sobre la degradación de los arrecifes coralinos: Una revisión para la República Dominicana. AULA Revista de Humanidades y Ciencias Sociales 68:31–60 https://doi.org/1033413/aulahcs.2022.68i1.194

Croquer, A., A. Banaszak, and M. Vermeij. 2022c. *Eusmilia fastigiata*. The IUCN Red List of Threatened pecies 2022:e.T133400A165869793. https://doi.org/10.2305/IUCN.UK.2022–2.RLTS.T133400A165869793.en. (viewed on 10/31/2023)

de Bakker, D.M., F.C. Van Duyl, R.P.M. Bak, M.M. Nugues, G. Nieuwland, and E.H. Meesters. 2017. 40 years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: The rise of slimy cyanobacterial mats. Coral Reefs 36:355–367. https://doi.org/10.1007/s00338–016–1534–9

Eakin, C.M., J.A. Morgan, S.F. Heron, T.B. Smith, G. Liu, L. Alvarez–Filip, B. Baca, E. Bartels, C. Bastidas, C. Bouchon, M. Brandt, A.W. Bruckner, L. Bunkley–Williams, A. Cameron, B.D. Causey, M. Chiappone, T.R.L. Christensen, M.J.C Crabbe, O. Day, E. de la Guardia, G. Díaz–Pulido, D. DiResta, D.L. Gil–Agudelo, D.S. Gilliam, R.N. Ginsburg, S. Gore, H.M. Guzmán, J.C. Hendee, E.A. Hernández–Delgado, E. Husain, C. Jeffrey, R.J. Jones, E. Jordán–Dahlgren, L.S. Kaufman, D.I. Kline, P.A. Kramer, J. Lang, D. Lirman, J. Mallela, C. Manfrino, J. Maréchal, K. Marks, J. Mihaly, W. Miller, E. Mueller, E. Muller, C. Orozco Toro, H.A. Oxenford, D. Ponce–Taylor, N. Quinn, K. Ritchie, S. Rodríguez, A. Rodríguez, S. Romano, J. Samhouri, J. Sánchez, G. Schmahl, B.V. Shank, W. Skirving, S. Steiner, E. Villamizar, S.M. Walsh, C. Walter, E. Weil, E.H. Williams, K. Woody Roberson, and Y. Yusuf. 2010. Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. PloS One 5(11): e13969. https://doi.org/10.1371/journal.pone.0013969

Estrada–Saldívar, N., B.A. Quiroga–García, E. Pérez–Cervantes, O.O. Rivera–Garibay, and L. Alvarez–Filip. 2021. Effects of the stony coral tissue loss disease outbreak on coral communities and the benthic composition of Cozumel reefs. Frontiers in Marine Science 8:632777. https://doi.org/10.3389/fmars.2021.632777

Ford A.K., S. Bejarano, M.M. Nugues, P.M.Visser, S. Albert, and S.C.A. Ferse. 2018. Reefs under siege–the rise, putative drivers, and consequences of benthic cyanobacterial mats. Frontiers in Marine Science 5:18. https://doi.org/10.3389/fmars.2018.00018

Gardner, T.A., I.M. Côté, J.A. Gill, A. Grant, and A.R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long–term decline. Ecology 86:174–184. https://doi.org/10.1890/04–0141

Gintert, B.E., W.F. Precht, R. Fura, K. Rogers, M. Rice, L.L. Precht, M. D'Alessandro, J. Croop, C. Vilmar, and M.L. Robbart. 2019. Regional coral disease outbreak overwhelms impacts from a local dredge project. Environmental Monitoring and Assessment 191:630. https://doi.org/10.1007/s10661–019–7767–7

Gochfeld, D.J., J.B. Olson, A. Chaves–Fonnegra, T.B. Smith, R.S. Ennis, and M.E. Brandt. 2020. Impacts of hurricanes Irma and Maria on coral reef sponge communities in St. Thomas, US Virgin Islands. Estuaries and Coasts 43:1235–1247. https://doi.org/10.1007/s12237–020–00694–4

Goldenberg, S.B., C.W. Landsea, A.M. Mestas–Nuñez, and W.M. Gray. 2001. The recent increase in Atlantic hurricane activity: Causes and implications. Science 293:474–479. https://doi.org/10.1126/science.1060040

Green, E.P. and A.W. Bruckner. 2000. The significance of coral disease epizootiology for coral reef conservation. Biological Conservation 96:347–361. https://doi.org/10.1016/S0006–3207(00)00073–2

Hayes N.K., C.J. Walton, and D.S. Gilliam. 2022. Tissue loss disease outbreak significantly alters the southeast Florida stony coral assemblage. Frontiers in Marine Science 9:975894. https://doi.org/10.3389/fmars.2022.975894

Heron, S., J. Morgan, M. Eakin, and W. Skirving. 2008. Hurricanes and their effects on coral reefs. In: C. Wilkinson and D. Souter, eds. Status of Caribbean Coral Reefs after Bleaching and Hurricanes in 2005. Global Coral Reef Monitoring Network, and Reef and Rainforest Research Centre, Townsville, Australia, p. 31–36. https://portals.iucn.org/library/node/9411

Hughes, T.P. 1994. Catastrophes, phase shifts, and large–scale degradation of a Caribbean coral reef. Science 265:1547–1551. https://doi.org/10.1126/science.265.5178.1547

Irazabal, I. and M. Rodríguez. 2019. First report of Stony Coral Tissue Loss Disease in the Dominican Republic. Atlantic and Gulf Rapid Reef Assessment, Dominican Republic. https://www.agrra.org/front–page–news/sctlddomrep/ (viewed on 10/15/2024)

IUCN Red List of Threatened Species. 2023. https://www.iucnredlist.org/en. (viewed on 10/05/2023)

Jury, M.R., R. Rios–Berrios, and E. García. 2012. Caribbean hurricanes: Changes of intensity and track prediction. Theoretical and Applied Climatology 107:297–311. https://doi.org/10.1007/s00704–011–0461–5

Kuta, K. and L.J.C.R. Richardson. 2002. Ecological aspects of black band disease of corals: Relationships between disease incidence and environmental factors. Coral Reefs 21:393–398. https://doi.org/10.1007/s00338–002–0261–6

Legendre, P. and M.J. Anderson. 1999. Distance–based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69:1–24. https://doi.org/10.1890/0012–9615(1999)069[0001:DBRATM]2.0.CO;2

Madden, I.A., A. Mariwala, M. Lindhart, S. Narayan, K.K. Arkema, M.W. Beck, J.W. Baker, and J. Suckale. 2023. Quantifying the fragility of coral reefs to hurricane impacts: A case study of the Florida Keys and Puerto Rico. Environmental Research Letters 18(2):024034. https://doi.org/10.1088/1748–9326/acb451

Martinez, S.J., F. Cavada–Blanco, J. Cappelletto, E. Agudo–Adriani, and A. Croquer. 2021. Distribution, abundance, and health indicators of the critically endangered coral species *Acropora cervicornis* in Los Roques National Park, 2014. Advances in Oceanography and Limnology 12(2):10005. https://doi.org/10.4081/aiol.2021.10005

Miller, J., E. Muller, C. Rogers, R. Waara, A. Atkinson, K.R.T. Whelan, and B. Witcher. 2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. Coral Reefs 28:925–937. https://doi.org/10.1007/s00338–009–0531–7

Miyazawa, E., L.M. Montilla, E.A. Agudo–Adriani, A. Ascanio, G. Mariño–Briceño, and A Croquer. 2020. On the importance of spatial scales on beta diversity of coral assemblages: A study from Venezuelan coral reefs. PeerJ 8: e9082. https://doi.org/10.7717/peerj.9082

Navas–Camacho, R., D.L. Gil–Agudelo, A. Rodríguez–Ramírez, M.C. Reyes–Nivia, and J. Garzón–Ferreira. 2010. Coral diseases and bleaching on Colombian Caribbean coral reefs. Revista de Biología Tropical 58:95–106. https://doi.org/10.15517/rbt.v58i1.20026

Neely, K.L., C.L. Lewis, K.S. Lunz, and L. Kabay. 2021. Rapid population decline of the pillar coral *Dendrogyra cylindrus* along the Florida Reef Tract. Frontiers in Marine Science 8:434. https://doi.org/10.3389/fmars.2021.656515

Precht W.F., B.E. Ginter, M.L. Robbart, R. Fura and R. van Woesik. 2016. Unprecedented disease–related coral mortality in southeastern Florida. Science Reports 6:31374. https://doi.org/10.1038/srep31374

Randazzo–Eisemann, Á., J.R. Garza–Pérez, I. Penié–Rodriguez, and B. Figueroa–Zavala. 2021. 25 years of multiple stressors driving the coral–algae phase shift in Akumal, Mexico. Ocean & Coastal Management 214:105917. https://doi.org/10.1016/j.ocecoaman.2021.105917

Richardson, L.L. and J.D. Voss. 2005. Changes in a coral population on reefs of the northern Florida Keys following a coral disease epizootic. Marine Ecology Progress Series 297:147–156. https://doi.org/10.3354/meps297147

Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series 62:185–202. https://doi.org/10.3354/meps062185

Rogers, C.S. and C.E. Ramos–Scharrón. 2022. Assessing effects of sediment delivery to coral reefs: A Caribbean watershed perspective. Frontiers in Marine Science 8:773968. https://doi.org/10.3389/fmars.2021.773968

Rousseau, Y., R. Galzin, and J.P. Marechal. 2010. Impact of hurricane Dean on coral reef benthic and fish structure of Martinique, French West Indies. Cybium 34:243–256.

Sellares–Blasco, R.I., A. Croquer, M.F. Villalpando, A. Valdez–Trinidad, O. Shamir, J. Delance, S.A. King–Perez, and S.D. Guendulain–Garcia. 2023. First quantitative assessment of benthic and fish assemblages of Silver Bank, Dominican Republic. Caribbean Journal of Science 53:258–273. https://doi.org/10.18475/cjos.v53i2.a9

Sokolow, S. 2009. Effects of a changing climate on the dynamics of coral infectious disease: A review of the evidence. Diseases of Aquatic Organisms 87:5–18. https://doi.org/10.3354/dao02099

Steneck, R.S. and R. Torres. 2023. Trends in Dominican Republic coral reef biodiversity 2015–2022. Diversity 15:389. https://doi.org/10.3390/d15030389

Villalpando, M.F., S.D. Guendulain–García, A. Valdez–Trinidad, A. Croquer, and R.I Sellares–Blasco. 2022. Coral reefs of southeastern Dominican Republic hit by two simultaneous epizootic events. Bulletin of Marine Science 98:507–508. https://doi.org/10.5343/bms.2022.0015

Voss, J.D. and L.L. Richardson. 2006. Nutrient enrichment enhances black band disease progression in corals. Coral Reefs 25:569–576. https://doi.org/10.1007/s00338–006–0131–8

Weber, M., D. De Beer, C. Lott, L. Polerecky, K. Kohls, R.M. Abed, and K.E. Fabricius. 2012. Mechanisms of damage to corals exposed to sedimentation. Proceedings of the National Academy of Sciences 109:E1558–E1567. https://doi.org/10.1073/pnas.1100715109

Weil, E. 2004. Coral reef diseases in the wider Caribbean. In: E. Rosenberg E. and Y. Loya, eds. Coral Health and Disease. Springer, Berlin, Heidelberg, Germany, p. 35–68. https://doi.org/10.1007/978–3–662–06414–6_2

Weil, E. and A. Cróquer. 2009. Spatial variability in distribution and prevalence of Caribbean scleractinian coral and octocoral diseases. I. Community–level analysis. Diseases of Aquatic Organisms 83:195–208. https://doi.org/10.3354/dao02011

Weil, E. and C.S. Rogers. 2010. Coral reef diseases in the Atlantic–Caribbean. In: Z. Dubinsky and N. Stambler, eds. Coral Reefs: An Ecosystem in Transition. Springer, Dordrecht, The Netherlands, p. 465–491. https://doi.org/10.1007/978–94–007–0114–4_27

Weil, E., G. Smith, and D.L. Gil–Agudelo. 2006. Status and progress in coral reef disease research. Diseases of Aquatic Organisms 69:1–7. http://goi.org/10.3354/dao069001

Weil, E., A. Cróquer, and I. Urreiztieta. 2009a. Yellow band disease compromises the reproductive output of the Caribbean reef–building coral *Montastraea faveolata* (Anthozoa, Scleractinia). Diseases of Aquatic Organisms 87:45–55. https://doi.org/10.3354/dao02103

Weil, E., A. Croquer, and I. Urreiztieta. 2009b. Temporal variability and impact of coral diseases and bleaching in La Parguera, Puerto Rico from 2003–2007. Caribbean Journal of Science 45:221–246. https://doi.org/10.18475/cjos.v45i2.a10

Williams, S.M., J. García–Sais, and J. Sabater–Clavell. 2021. Prevalence of stony coral tissue loss disease at El Seco, a mesophotic reef system off Vieques Island, Puerto Rico. Frontiers in Marine Science 8:668669. https://doi.org/10.3389/fmars.2021.668669