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RESEARCH

Tipping the balance: reef community shifts after a regional urchin population collapse

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Abstract Coral reef ecosystems are maintained by complex interactions among organisms, with herbivory playing a critical role in regulating benthic algae populations and preserving reef health. Herbivores such as the black spiny sea urchin, *Diadema antillarum*, prevent macroalgae from outcompeting corals by exerting top-down control, sustaining ecosystem stability and diversity. There is evidence that the mass mortality of *D. antillarum* in the 1980s contributed to phase shifts from coral-dominated to algal-dominated states across the Caribbean, demonstrating their critical role in reef dynamics. Certain areas of the Caribbean experienced a slow recovery of *Diadema*, until 2022, when another mass mortality event occurred. This study investigates the ecological impacts of the recent 2022 die-off using monitoring data collected from Culebra, Puerto Rico, between 2021 and 2024. High-resolution orthomosaics generated through photogrammetry and Structure-from-Motion (SfM) techniques were used to assess shifts in benthic community structure, with a focus on changes in algal and coral cover in response to *D. antillarum* density. We documented a severe decline in *D. antillarum* densities, following the 2022 die-off event, with reductions of up to 99% across surveyed sites. Our results also showed increases in algal cover and decreases in sponge cover following the loss of *D. antillarum,* highlighting the potential community assembly regulative role of this herbivore. These findings underscore the urgency of protecting and restoring key herbivore species and highlight the need for targeted management strategies to mitigate further degradation of Caribbean reef systems.

Keywords Photogrammetry · Algae proliferation · Benthic community structure · Herbivore loss · Coral-algal competition · Reef degradation

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The original article has been updated. In the original version of this article, the given and family names of all authors in the authors list were incorrectly structured. The names were displayed correctly in all versions at the time of publication.

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Introduction

Coral reef ecosystems are shaped by complex interactions among organisms, with herbivory playing a crucial role in maintaining reef health (Adam et al. 2015, 2022; Mumby et al. 2006). Herbivores, such as sea urchins, help regulate algal populations, preventing macroalgae from outcompeting corals for space and light (Adam et al. 2022). This regulation is essential for maintaining healthy competition dynamics and reef resilience, particularly in the face of stressors like increasing anthropogenic disturbances and climate change (Barott et al. 2012; Burkepile & Hay 2008; Cramer et al. 2021. When herbivore populations decline, macroalgae can proliferate, potentially leading to phase shifts where reefs transition from coral-dominated to algal-dominated states (Dudgeon et al. 2010; Hughes 1994; Hughes et al. 2007). These interactions are further complicated by feedback loops involving nutrient dynamics, predator–prey relationships, and species-specific functional roles (Adam et al. 2015; Alvarez-Filip et al. 2011; Arnold et al. 2010). The balance between herbivory and algal growth plays a significant role in determining reef community structure and function, highlighting the importance of protecting key herbivores to sustain ecosystem stability and biodiversity.

In the 1980's Caribbean reefs experienced a mass mortality event of the black spiny sea urchin, *Diadema antillarum* (*Diadema* hereafter), a key herbivore on Caribbean reefs (Carpenter 1990; Mumby et al. 2006). The die-off reduced *Diadema* densities across the western Atlantic by over 97%, contributing to, and further accelerating, phase shifts from coral-dominated to algal-dominated communities in many reefs (Lessios 2016; Mumby et al. 2006). Without the grazing pressure of *Diadema*, macroalgae rapidly proliferated, reaching densities high enough to overgrow and smother even adult coral colonies (Lessios 2016).

Following the catastrophic mass mortality of *Diadema* in the 1980s, populations remained depressed for decades, with only isolated signs of recovery observed in parts of the Caribbean by the mid-2010s (Lessios 2016). However, in 2022, another widespread mortality event of *Diadema* swept across the eastern Caribbean, marking the most significant die-off of this keystone herbivore since the catastrophic 1983 event (Hylkema et al. 2023). First reported in the Virgin Islands, the die-off spread rapidly across multiple reef systems, with *Diadema* exhibiting characteristic symptoms such as spine loss, disorientation, and rapid tissue degradation before succumbing to mortality by a scuticociliate (Hewson et al. 2023; Hylkema et al. 2023). Given the species' critical role in reef herbivory, this event raises concerns about the potential for increased macroalgal dominance and further reef degradation, particularly in systems where *Diadema* had begun to recover (Burkepile & Hay 2008; Lessios 2016; Williams 2022). The 2022 die-off underscores the vulnerability of *Diadema* populations and highlights the urgency of understanding the drivers and ecological consequences of such mortality events in present day reefs.

Evaluating the impacts of the 2022 *Diadema* die-off is essential for understanding the importance of their slow recovery and the resilience of today's coral reef ecosystems. As with the mass mortality event in 1983, contemporary reefs continue to face compounding stressors such as climate change, ocean acidification, and the decline of herbivorous species due to overfishing and disease (Alvarez-Filip et al. 2022; Barott et al. 2012; Cramer et al. 2021; Hughes et al. 2007). However, unlike in the past, *Diadema* now persists at relatively low densities, raising important questions about the extent of their current ecological role. Although their loss is concerning, the influence of *Diadema* on reef dynamics may not be as pronounced as it once was. Nonetheless, their continued decline could further hinder coral recruitment and accelerate shifts in benthic community composition and structure (Adam et al. 2022; Arnold et al. 2010; Carpenter 1990; Rodríguez-Barreras et al. 2018). Given that some *Diadema* populations had shown signs of recovery prior to this event, their sudden decline raises concerns about whether natural recolonization can still occur under present-day conditions (Rogers & Lorenzen 2016). Investigating the ecological consequences of this die-off will provide insights into the role of *Diadema* in reef dynamics under current altered conditions, the potential for recovery, and the management strategies needed to mitigate further ecosystem decline.

Monitoring efforts using large-area images via photogrammetry can provide detailed (i.e., high-resolution) and diverse ecological information critical to understanding the role of herbivores, such as *Diadema,* in regulating the community assembly on reefs. These large-area images allow us to quantify changes in algal and coral cover over time and assess how the loss of this key herbivore influenced benthic community structure. For this study, we used large-area images created as part of a monitoring effort in the municipal island of Culebra (Puerto Rico) to specifically ask: 1) Are there signs of *Diadema* recovery? 2) How did the benthic community structure respond to the *Diadema* die-off? And 3) How does algae cover relate to urchin density in modern-day reefs?

Given the strong herbivory pressure exerted by *Diadema*, we hypothesized that sites with previously high urchin densities would experience a more pronounced shift toward algae-dominated communities than those where *Diadema* was already scarce or absent. In the absence of these grazers, macroalgae are expected to proliferate, potentially outcompeting corals and altering habitat structure. Modeling work by Mumby et al. (2006) identified the importance of high *Diadema* densities needed to prevent algal phase shifts.

To better understand these transitions, we assessed not only coral cover but also recruitment of the weedy coral *Porites astreoides*, as reduced herbivory may limit the settlement and survival of juvenile corals (Darling et al. 2012). Consequently, we hypothesized a shift in benthic community structure following the die-off, characterized by increased algal cover, reduced coral recruitment and cover. Together, these metrics provide insights into the mechanisms driving reef change and the potential for recovery in the face of mounting anthropogenic stressors and climate change.

Methods

Benthic monitoring

Data for this study was collected in Culebra, Puerto Rico, over 3 years (2021 to 2023). A total of 24 sites over two adjacent locations (Punta Maguey and Punta Tampico) were established on the south-western end of the island (Fig. 1). Each site consisted of four 100 m^2 plots ($n = 96$ total plots), which were delineated with nails and paracord in 2021 for consistent monitoring. Data from each individual plot was used for all statistical analyses. For this study, our time points consisted of a Pre-die-off (2021), Early-die-off (June/July 2022, right after the *Diadema* mortality event in Puerto Rico), Post-die-off (October 2022), and 1-year-post (May 2023) period.

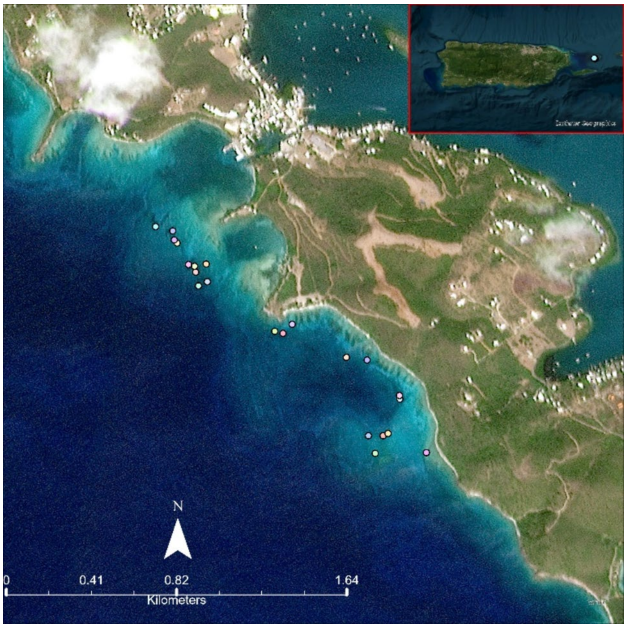

Fig. 1 Map of Culebra, Puerto Rico, showing the locations of study sites surveyed for benthic community structure and urchin density. Sites were monitored across four time periods to assess temporal dynamics in reef conditions

We used photogrammetry and Structure-from-Motion (SfM) techniques to generate high-resolution digital large-area images of benthic communities (Petrovic et al. 2014; Remmers et al. 2023). In 2021, images were collected using two GoPro Hero 8 cameras, whereas in subsequent years, we used two Nikon D7500 high-resolution cameras to follow monitoring protocols established by the National Oceanographic and Atmospheric Administration (Suka et al. 2019). Divers followed a non-disruptive lawn-mower survey pattern, maintaining an altitude of approximately 1.5 m above the reef substrate to ensure consistent image acquisition and minimize distortion. Images were captured with 70–80% overlap to facilitate accurate reconstruction. Eight scale bars were strategically placed within the survey area, and corresponding depth measurements were recorded. The collected images were color corrected in Adobe Lightroom and processed in Agisoft Metashape Pro (v2.0), where they were aligned, key points were matched, and a dense point cloud was generated following Cook et al., (2023). This point cloud was then used to create a two-dimensional orthomosaic or large-area Image (LAI), which served as the basis for the benthic analysis of this study.

Assessment of urchin density and benthic community response

Benthic community structure was quantified using percent cover estimates via the virtual point intercept method. LAIs were imported into ArcGIS, where they were overlaid with a 1 m^2 grid to divide the LAI into uniform sections. Each grid cell was extracted as a 1 m^2 image (photo-quadrat), resulting in a total of 95 to 165 photo-quadrats per reef plot, depending on the plot's actual size. Photo-quadrats were then uploaded to CoralNet for semi-automated image annotation (Williams et al. 2019). CoralNet uses convolutional neural networks trained on manually annotated images to classify benthic features, improving its accuracy over time through repeated exposure to manually labeled data. The model was trained with 23% of the uploaded photo-quadrats being manually annotated using 35 random points per 1 m x 1 m photo-quadrat on the LAI of the corresponding plot to classify benthic cover into 6 principal functional groups: hard coral, soft coral, algae, sponge, seagrass and sand, achieving an overall functional group accuracy of 80.2%. Species level identification and distinctions between macro and turf algae were excluded due to the model's inability to consistently distinguish between them accurately. This accuracy supports the reliability of the automated annotations in capturing broad patterns of benthic cover, although potential biases may still exist, particularly in underrepresented classes.

To assess shifts in *Diadema* density, we utilized the LAIs in place of direct field counts. Since urchins were not systematically counted during fieldwork, LAIs provided a critical *ex-situ* tool to approximate their presence and density across reef plots. Each LAI was examined for visible *Diadema* individuals. Individuals were tallied and divided by the area surveyed in each LAI to estimate urchin density per m^2. Different metrics, such as counting the number of urchin clusters and then binning them into categories, as well as counting individuals to measure urchin abundance, were also considered (SF. 1).

For coral recruitment estimates, point clouds generated during the LAI stitching process were imported into VISCORE software, scaled, and exported as orthoprojections (Petrovic et al. 2014). These orthoprojections were then analyzed in TagLab, where coral colonies of *Porites astreoides* were identified and delineated. *P. astreoides* was chosen due to its classification as a weedy coral – i.e., this species is currently expected to be doing well under current conditions (Darling et al. 2012). Recruitment was assessed by tracking the appearance of new colonies of *P. astreoides* between survey periods by counting new recruit size colonies in the Early-die-off and 1-year-post periods (i.e., small colonies not counted in late 2021 and 2022). Ortho-projection quality allowed us to assess individuals as small as 0.5 cm^2. To standardize measurements, recruits were limited to a maximum size of 5 cm^2.

Statistical analysis

All statistical analyses were conducted in R (v4.5.1; R Core Team, 2025) to examine temporal changes in *Diadema* density and the response of the benthic community to the die-off. The same plots within each site were resampled across sampling periods; plots were treated as subsamples within sites rather than as independent experimental units. We used generalized linear mixed models (GLMMs) to model the change in urchin density over time. The GLMM was fitted using a Tweedie error distribution and a log link, with site included as a random effect (Eq. 1). A Tweedie distribution was selected because urchin density data were continuous, non-negative, and right-skewed, with many low values and occasional zeros.

$$Urchinabundance \sim period + (1|site) \tag{1}$$

The response of the benthic community structure to the Diadema die-off was assessed using a multivariate analysis framework at the level of functional groups, including corals, algae, sponges, and seagrass. We conducted a Permutational Multivariate Analysis of Variance (PERMANOVA) using a Bray–Curtis dissimilarity matrix to evaluate differences in community structure across time periods (treated as a fixed effect). To account for spatial non-independence among samples, we specified site as a permutation stratum in the adonis2 function, constraining permutations to occur only within sites. This approach constrained permutations within sites, helping control site-level variation while testing the main effect of period. Because PERMANOVA can be sensitive to heterogeneity of multivariate dispersion, we tested for differences in dispersion among periods using PERMDISP (betadisper in vegan) with 999 permutations. Additionally, we conducted pairwise PERMANOVA comparisons among time periods to identify specific temporal shifts in community structure. Multivariate analyses were performed in R using the vegan package for adonis2 (Oksanen et al. 2001).

Generalized linear mixed models (GLMMs) with a Gaussian error distribution and an identity link were used to test whether changes in recruitment abundance (expressed as log response ratios) from Early-die-off to 1-year-post were predicted by Pre-die-off *Diadema* density, including site as a random effect (Eq. 2). A Gaussian error distribution with an identity link was chosen because the log response ratios were continuous and approximately normally distributed.

$$LRR_x \sim Diademadensity_{Pre-die-off} + (1|site) \tag{2}$$

Change in recruitment was quantified using two approaches. First, as a log response ratio (Eq. 3) describes changes relative to baseline conditions. Second, to formally test whether recruitment differed before and after the die-off, recruit counts were summed across plots within each site and analyzed using a negative binomial GLM with period as a fixed effect. Sites were treated as independent replicates, and a negative binomial distribution was used to account for overdispersion in the count data. The log response ratio (*LRR*) was calculated using the following formula

$$LRR_x = \log\frac{x_{post}}{x_{pre}} \tag{3}$$

where x_{post} is the post die-off value for the response variable of interest x and x_{pre} is the Pre-die-off value for response variable x.

Additionally, the log-ratio of algal change was modeled using a Gaussian error distribution and an identity link, with initial *Diadema* density as a fixed effect and site as a random effect. Log response ratios (LRRs) were used to quantify proportional change through time, providing a scale-independent and symmetric measure of increase or decline. Similarly, the log response ratio of sponge cover was modeled using a GLMM with a Gaussian distribution and identity link, with pre-die-off *Diadema* density as predictor variables and site as a random effect to evaluate their influence on sponge cover change.

We used GLMMs with beta error distribution (i.e., beta regressions) to assess changes in coral, algae, and sponge percent cover across periods (Pre-die-off, Early-die-off, Post-die-off and 1-year-post), with period as a fixed effect and site as a random intercept to account for site-level variability (Eq. 4). Beta regression was selected because percent cover is a continuous, bounded variable (0–1).

$$\%cover_{coral,sponge,macroalgae} \sim period + (1|site) \quad (4)$$

Model diagnostics and simplification were conducted using the performance package (Lüdecke et al. 2021) to evaluate model fit and verify assumptions. Model selection was refined through dredging with the MuMIn package (Bartoń, 2010), and candidate models were ranked by AICc. Models within ΔAICc < 4 were retained as the top set of competing models, from which we selected the most parsimonious model that included at least one predictor variable. In cases where multiple predictors were supported, we compared their relative contribution and retained the model with the lowest AICc, greatest model weight and highest conditional R^2.

Results

Diadema die-off

Our study revealed a decline in *Diadema antillarum* density across the study area following the 2022 die-off event (Fig. 2a). Model predictions from a Tweedie mixed-effects model (with a log link and site as a random effect) showed an approximately 99% reduction in mean urchin density immediately after the die-off (Type II Wald $\chi^2 = 147.5$, df = 3, $p < 0.001$). Mean predicted densities declined from 0.026 urchins m^{-2} before the die-off (Pre-die-off; 95% CI = 0.010–0.068) to 0.00046 urchins m^{-2} during the Early-die-off period (95% *CI* = 0.00012–0.0017). The lowest densities occurred Post-die-off (0.000085 urchins m^{-2}, 95% CI = 0.000014–0.00051). Pairwise comparisons confirmed that all post-die-off periods differed significantly from Pre-die-off ($z \geq 7.1$, $p < 0.0001$, Tukey-adjusted), whereas differences among the post-die-off periods themselves were not significant ($z \leq 2.0$, $p \geq 0.09$) (Table 1 and S1; Fig. 2a).

Benthic community structure response to die-off (multivariate analysis)

Our multivariate analysis indicated significant temporal changes in benthic community structure following the die-off (Fig. 3). PERMANOVA revealed a significant effect of period on community structure ($R^2 = 0.0812$, $F = 10.607$, $p = 0.001$), explaining 8.12% of the total variation (Table 2 and S2). Pairwise comparisons showed that the Pre-die-off period differed significantly from all subsequent periods (Pre-die-off vs. Early-die-off: $R^2 = 0.1159$, F = 23.33, $p = 0.001$; Pre-die-off vs. Post-die-off: $R^2 = 0.0924$, $F = 18.02$, $p = 0.001$; Pre-die-off vs. 1-year-post: $R^2 = 0.0611$, F = 11.92, $p = 0.001$). In contrast, community structure did not differ significantly between Early-die-off and Post-die-off periods ($p = 0.111$), nor between Post-die-off and 1-year-post ($p = 0.254$), although Early-die-off and 1-year-post differed significantly ($p = 0.026$).

Tests of multivariate dispersion indicated significant differences in within-period variability among periods (PERMDISP: F = 6.32, $p = 0.001$).

Benthic functional group response to die-off (univariate analysis)

Univariate analyses from the benthic data extracted with CoralNet revealed temporal changes in the benthic cover of functional groups, often correlated with urchin density. Coral percent cover increased following the *Diadema* die-off. Model-predicted mean coral cover rose from 1.26% (95% CI = 1.02–1.54) during the Pre-die-off period to 1.48% (95% CI = 1.21–1.81) in the Early-die-off period ($z = 2.69$, $p = 0.007$), representing a ~ 17% relative (0.22 percentage-point) increase. Coral cover during the Post-die-off period showed a non-significant change to 1.31% (95% CI = 1.07–1.61; $z = 0.66$, $p = 0.51$; + 4%), while the 1-year-post period increased to 1.51% (95% CI = 1.23–1.85; $z = 3.04$, $p = 0.002$) a ~ 20% relative (0.25 percentage-point) gain compared to the Pre-die-off period (Fig. 4a, Table 3 and S3).

Algae percent cover increased significantly following the *Diadema* die-off. A beta-regression mixed model (site as a random effect) detected a strong effect of period on algal cover ($\chi^2 = 22.45$, $df = 3$, $p < 0.001$). Model-predicted algal mean cover rose from 25.2% (95% CI = 21.4–29.4) during the Pre-die-off period to 31.6% (95% CI = 27.2–36.3) in the Early-die-off period ($z = 4.62$, $p < 0.001$), representing a 25% relative (6.4-percentage-point) increase. Algae cover remained elevated thereafter, averaging 29.6% (95% CI = 25.4–34.2; $z = 3.28$, $p = 0.001$; + 18%, + 4.4 points) during the Post-die-off period and 28.6% (95% CI = 24.5–33.1; $z = 2.56$, $p = 0.011$; + 14%, + 3.4 points) 1-year-post (Fig. 4b, Table 3 and S3). Sponge percent cover declined following the *Diadema* die-off. A beta-regression mixed model (site as a random effect) revealed a strong effect of period on sponge cover ($\chi^2 = 204.26$, $df = 3$, $p < 0.001$). Model-predicted mean sponge cover decreased from 5.0% (95% CI = 4.2–6.0) Pre-die-off to 1.5% (95% CI = 1.2–1.9) in the Early-die-off period ($z = 11.85$, $p < 0.001$), representing a 70% relative (3.5 percentage-point) reduction. Sponge cover remained low in the post-die-off period (1.6%, 95% CI = 1.3–2.0; $z = 11.23$, $p < 0.001$) and showed an increase by 1-year-post (2.2%, 95% CI = 1.8–2.7; $z = 8.92$, $p < 0.001$). Although the small recovery at 1-year

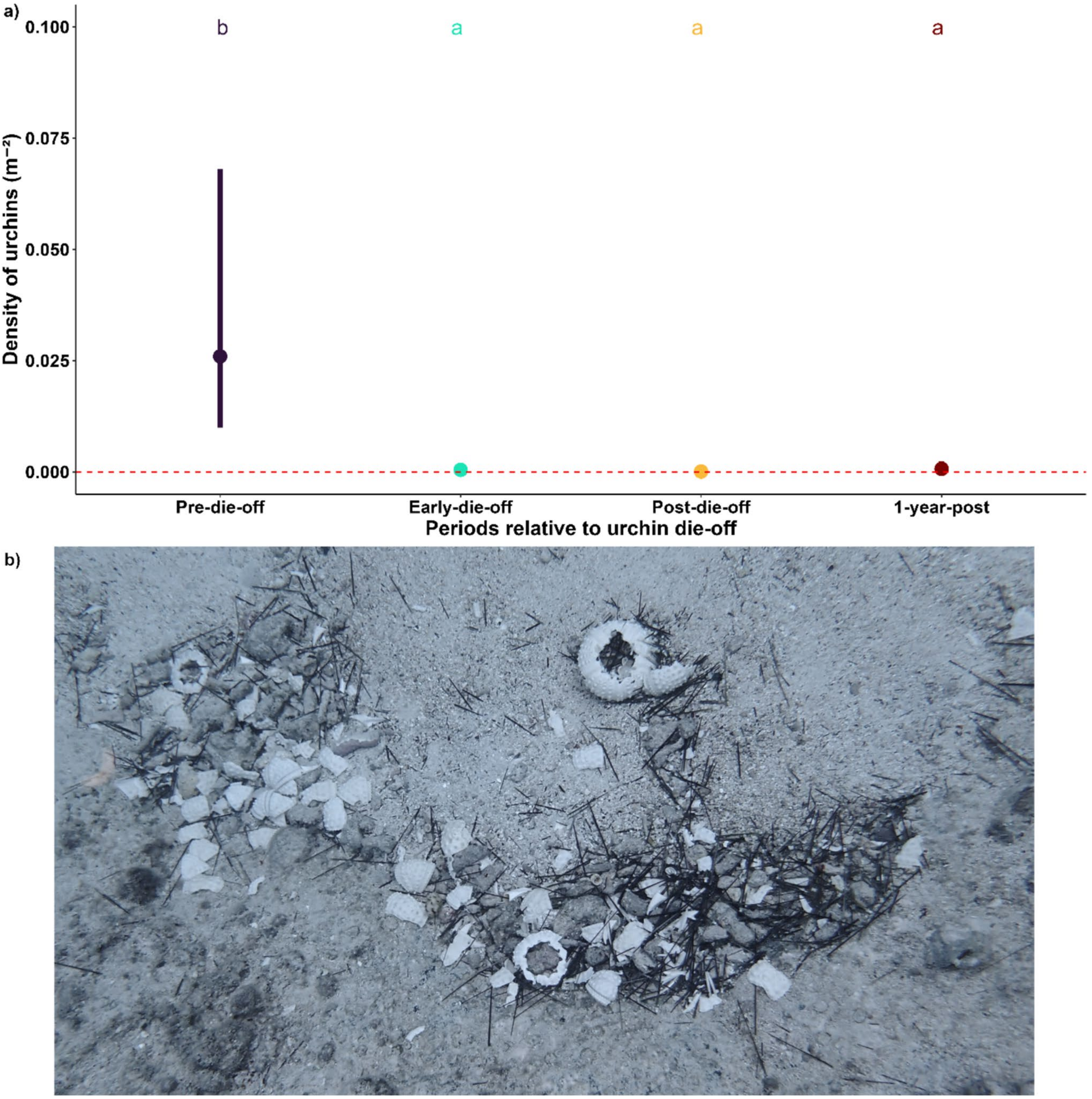

Fig. 2 Changes in Diadema antillarum density before and after the mass mortality event. **a** Mean number of urchins per m^2 with 95% confidence intervals. Different letters indicate significant pairwise differences between periods (Tukey-adjusted, $p < 0.05$). **b** Photograph taken during study period showing multiple diseased Diadema

post-die-off was statistically significant relative to the immediately post-die-off periods ($z = 3.00$–3.50, $p \leq 0.014$), sponge cover remained below pre-die-off levels, indicating a sustained decline in benthic sponge abundance (Fig. 4c, Table 3 and S3).

Relationships between urchin density and change in algae cover and coral recruitment

The model selection process identified the Pre-die-off predictor variable as the top candidate model explaining variation in the log response ratio of *Porites astreoides* recruit density. The model incorporating urchin density provided the best overall fit and more stable

Table 1 Fixed and random effects from generalized linear mixed models examining the effects of time (period) on urchin density

Model	Term	Estimate	Std. Error	z value	p-value
Urchin density	(Intercept)	−4.167	0.492	−8.477	<0.001
Urchin density	Period Early-die-off	−4.038	0.521	−7.755	<0.001
Urchin density	Period Post-die-off	−5.724	0.808	−7.081	<0.001
Urchin density	Period 1-year-post	−3.641	0.461	−7.890	<0.001
Model	Term	Variance	Std. Dev		
Urchin density (random)	Site (Intercept)	3.379	1.838		

Period estimates are relative to the Pre-die-off period (intercept). Model was run with a Tweedie distribution

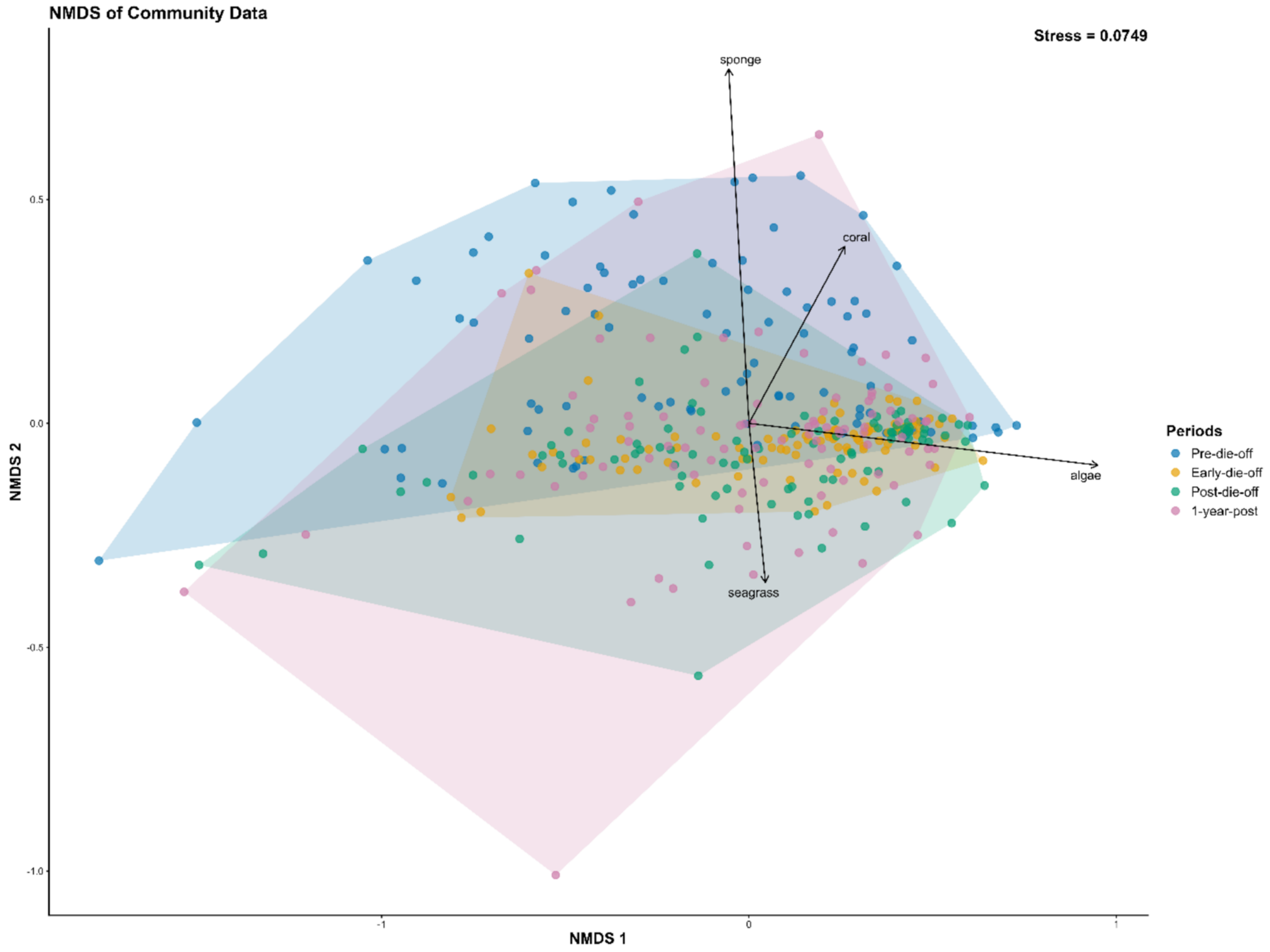

Fig. 3 Non-metric multidimensional scaling (NMDS) ordination of benthic community composition across four time periods relative to the Diadema die-off. Each point represents a plot in NMDS space based on Bray–Curtis dissimilarity. Colors indicate sampling periods. A stress value of 0.0749 indicates a good fit

diagnostics (AIC = 119.1 vs. 120.9; AIC weight = 0.72 vs. 0.28; conditional $R^2 = 0.34$ vs. 0.31). This Gaussian mixed-effects model (site as a random effect) revealed a negative trend between pre-die-off urchin density and the proportional change in *P. astreoides* recruit density; however, this relationship was not statistically significant ($\beta = -1.76 \pm 0.92$ SE, $z = -1.92$, $p = 0.055$) (ST 4, Fig. 5). Coral recruitment was significantly lower in Summer 2023 compared to the Baseline period (negative binomial GLM: $\beta = -1.02 \pm 0.27$ SE, $z = -3.82$, $p < 0.001$),

Table 2 PERMANOVA results testing differences in community composition across four time periods

Term	df	Sum of Squares	R^2	F-value	p-value
Period	3	1.844	0.081	10.607	0.0010
Residual	360	20.861	0.919		
Total	363	22.705	1.000		

corresponding to an approximately 64% reduction in site-level recruitment.

Our log-ratio model for algal cover, where the response represents the proportional change in algal cover relative to Pre-die-off levels (selected after model selection), revealed a significant positive relationship between Pre-die-off urchin density and subsequent increases in algal cover ($\beta = 0.824 \pm 0.383$ SE, $z = 2.16$, $p = 0.031$; $\chi^2 = 4.64$, $df = 1$). Plots with higher densities of urchins prior to the die-off experienced greater proportional increases in algal cover (Fig. 6).

Model dredging revealed that the null mixed-effects model provided the best support for sponge cover change following the *Diadema* die-off (AIC = 255.3), indicating that none of the evaluated fixed effects improved model fit. The Gaussian mixed-effects model, which included site as a random effect, showed a significantly negative intercept (Estimate = -1.37 ± 0.19 SE, $z = -7.16$, $p < 0.001$), reflecting an overall decline in sponge cover across sites.

Discussion

The loss of herbivores can trigger profound changes in community structure across ecosystems, including coral reefs. In Caribbean reef systems, *Diadema* historically played a critical role in maintaining competitive dynamics between coral and algae by grazing down fast-growing macroalgae (Carpenter 1990; Lessios 1988). When such herbivores are lost, there is a release from top-down control, allowing macroalgae to proliferate. In our study, the decline in *Diadema* density was followed by an increase in macroalgal cover, and a shift in benthic community structure. As macroalgae physically overgrow corals and other sessile invertebrates, they compete for space and light, while also releasing chemical compounds that can inhibit coral recruitment and growth, as well as alter microbial community dynamics (McCook et al., 2001; Rasher & Hay, 2010). These changes may further reduce coral resilience and contribute to long-term shifts in community composition. Similar dynamics have been observed in terrestrial systems; for instance, in African savannas, exclusion of large herbivores can result in woody plant encroachment that suppresses understory diversity through both physical and chemical interference (Pringle et al., 2023; Young et al., 2013). These cross-ecosystem parallels underscore the broad ecological importance of herbivores in regulating community dynamics and maintaining ecosystem functions. In the context of our findings, the disproportionate influence of *Diadema* on benthic community structure highlights its role not only as a grazer, but as a regulator of broader feedback loops that shape reef trajectories.

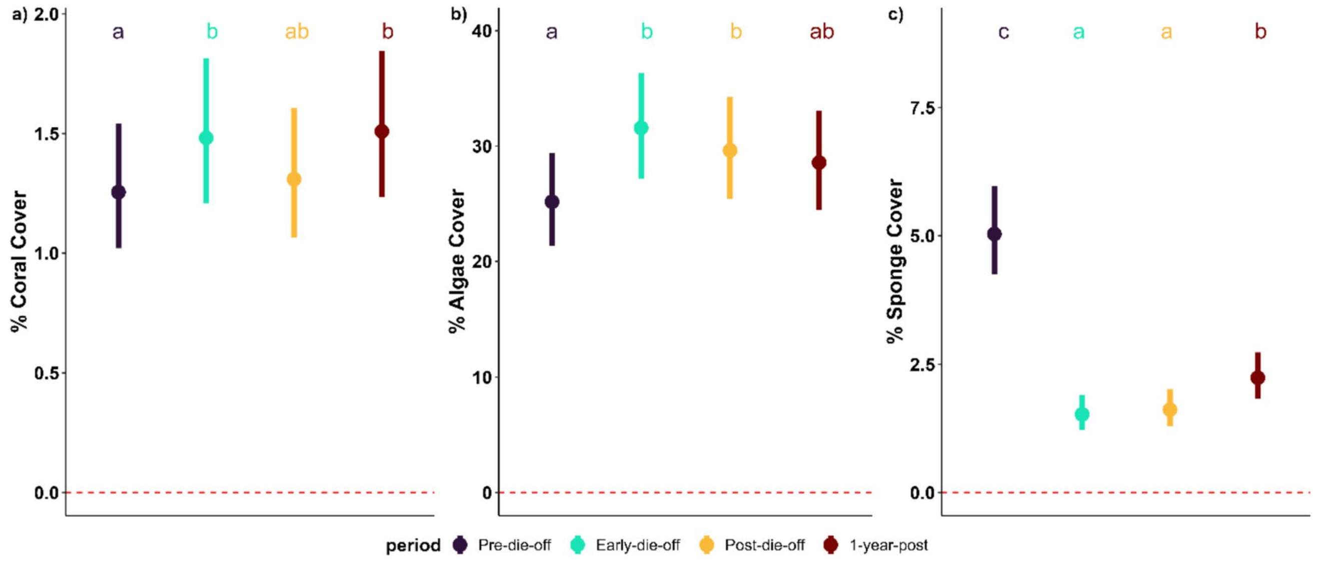

Fig. 4 Changes in percent cover of major benthic functional groups across four time periods relative to the Diadema die-off event. **a** Coral cover remained relatively stable. **b** Algae cover increased significantly after the die-off and remained elevated. **c** Sponge cover declined post-die-off, followed by a partial recovery. Points represent mean percent cover per period with 95% confidence intervals. Letters denote significant differences between time periods based on post hoc pairwise comparisons (Tukey-adjusted, $p < 0.05$)

Table 3 Fixed effects from beta regression models examining changes in percent cover of coral, algae, and sponge functional groups across time periods relative to the Pre-die-off

Model	Term	Estimate	Std. Error	z value	p-value
Coral cover	(Intercept)	−4.365	0.107	−40.956	< 0.0001
Coral cover	Period Early – die-off	0.168	0.063	2.686	0.0072
Coral cover	Period Post-die-off	0.043	0.064	0.664	0.5068
Coral cover	Period 1-year-post	0.187	0.061	3.041	0.0024
Algae cover	(Intercept)	−1.089	0.109	−9.974	< 0.0001
Algae cover	Period Early-die-off	0.316	0.068	4.622	< 0.0001
Algae cover	Period Post-die-off	0.224	0.068	3.275	0.0011
Algae cover	Period 1-year-post	0.173	0.068	2.555	0.0106
Sponge cover	(Intercept)	−2.937	0.092	−32.094	< 0.0001
Sponge cover	Period Early-die-off	−1.230	0.104	−11.849	< 0.0001
Sponge cover	Period Post-die-off	−1.171	0.104	−11.227	< 0.0001
Sponge cover	Period 1-year-post	−0.840	0.094	−8.925	< 0.0001
Model	Term	Variance	Std. Dev		
Coral cover (random)	Site (Intercept)	0.200	0.447		
Algae cover (random)	Site (Intercept)	0.208	0.456		
Sponge cover (random)	Site (Intercept)	0.110	0.331		

Positive values indicate an increase in cover relative to Pre-die-off, whereas negative values indicate a decline. All models include significant temporal effects, particularly for algae and sponge cover following the urchin die-off

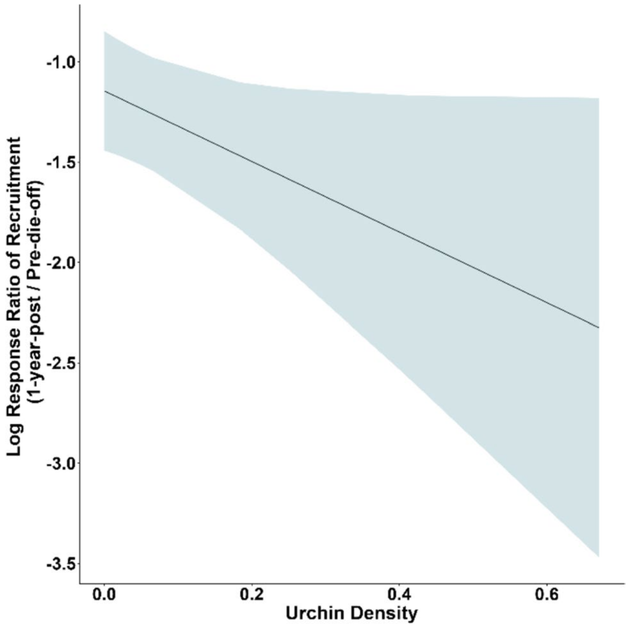

Fig. 5 Relationship between urchin density and changes in coral recruit abundance. Sites with higher pre-die-off Diadema density experienced greater declines in coral recruitment following the die-off event. Shaded areas represent 95% confidence intervals for the linear model

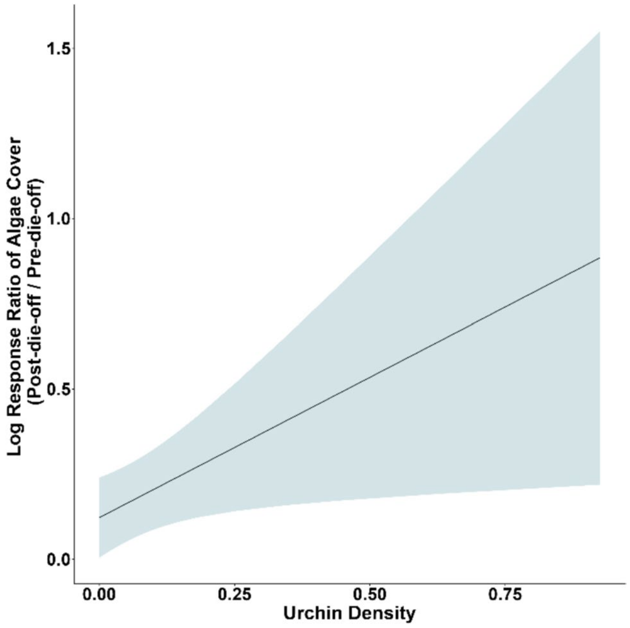

Fig. 6 Relationships between Pre-die-off urchin density and changes in algae cover following the Diadema die-off. Sites with a greater density of urchins at Pre-die-off exhibited significantly larger increases in algae cover. Shaded areas represent 95% confidence intervals

In our study, we assessed the response of the benthic community to the recent die-off of *Diadema* in Culebra, Puerto Rico. We documented a 99% decline in urchin density, comparable to the catastrophic 1980s die-off, when populations declined by approximately 98% (Carpenter 1988; Lessios 1988). A very slight increase in urchin density was observed in later periods of our study, specifically one year after the die-off, but this effect was not significant, and we believe these may not indicate proper recruitment but rather the movement of individuals from other locations. As Lessios (2016) suggests, *Diadema* populations have been observed to migrate following die-off events, likely in search of suitable habitat. Given the slow population recovery rates documented in previous studies, it is unlikely that the observed urchins represent new recruitment events (Lessios 2016; Rogers & Lorenzen 2016). Instead, this may reflect redistribution from adjacent areas, temporarily increasing local densities. However, during the last sampling event, small juvenile individuals were observed (Santos and Rivas, unpublished observations), suggesting a potential slow recovery through recruitment.

Our results also indicate that initial urchin density patterns played a key role in determining post-mortality algal responses. Increased multivariate dispersion following the die-off indicates greater spatial heterogeneity in benthic community responses, suggesting that reefs diverged in their post-disturbance trajectories rather than shifting uniformly. This heterogeneity likely reflects local differences in reef condition and residual grazing pressure following the loss of *Diadema*. Areas with higher Pre-die-off urchin densities experienced greater increases in algal cover following the die-off, suggesting that these sites were previously under stronger grazing pressure (i.e., top-down control) by *Diadema*. The loss of this grazing pressure likely facilitated a more pronounced algal expansion, which may have reduced space available for coral recruitment, although the latter trend was not statistically significant (Edmunds & Carpenter 2001; Williams 2022). These findings highlight the importance of urchin density in reef benthic dynamics and suggest that future recovery efforts should consider not only the number of urchins but also their spatial distribution and local density patterns (Burkepile & Hay 2008; Levitan et al. 2014; Williams 2016).

Changes in algal and sponge cover likely associated with the recent mortality event resulted in a shift in reef community structure, with impacts persisting beyond the initial decline. By linking the decline in urchin density to subsequent increases in algal cover and shifts in benthic community structure, our analyses reinforce the critical ecological function of *Diadema* in suppressing algal-dominated reef states (Williams 2022). Although coral cover appeared to increase over time, this trend is likely an artifact of sampling bias rather than actual biological recovery. Coral cover was already extremely low and point count methods are known to underestimate true values when cover is sparse (Pante & Dustan 2012; Rivas et al., in prep). Furthermore, given the ongoing degradation of coral reefs, decreasing larval supply, and the lack of observed recruitment that could drive coral expansion, it is unlikely that this increase reflects a true positive trajectory (Edmunds & Elahi, 2007; Hughes et al., 2010). In such sparse conditions, even small absolute changes can disproportionately influence percent cover estimates (Pante & Dustan 2012). Instead, the apparent increase in coral cover highlights the methodological and ecological challenges of tracking coral responses in systems that are already severely degraded. This underscores the importance of combining traditional survey methods with complementary approaches, such as high-resolution photogrammetry, long-term colony tracking, or recruitment assays, to better detect subtle trends in coral dynamics and avoid misinterpreting noise as recovery (Burns et al. 2015; P. Edmunds & Riegl 2020).

The community structure change captured by our analysis was driven by the increase in algae cover and decrease in sponge cover. Algae responded rapidly to the loss of *Diadema*, increasing in cover following the die-off and remaining elevated throughout the study. The stabilization of algae cover after Fall 2022 indicates a shift toward a sustained phase of elevated algal dominance, rather than a return to pre-die-off conditions, especially on the reefs that previously had a relatively higher density of urchins. These results highlight that even at the comparatively low *Diadema* densities observed prior to the 2022 event, far below those reported in the 1980s, urchins were exerting a meaningful grazing pressure. Their loss underscores the disproportionate ecological role *Diadema* can play in regulating algal proliferation, especially on already degraded or low-complexity reefs where alternative herbivory is limited (Edmunds & Carpenter 2001). Although the temporal patterns observed here are consistent with a release from grazing following the loss of *Diadema*, other herbivores, such as herbivorous fishes, also contribute to algal regulation on Caribbean reefs. We did not directly quantify herbivorous fish abundance or biomass in this study and thus cannot fully report on the relative contributions of other herbivores to the observed changes in reef community structure. However, similar patterns have been documented elsewhere in the Caribbean following the 1983–84 *Diadema* collapse, where reefs experienced long-term algal dominance that persisted for decades (Edmunds & Carpenter 2001; Mumby et al. 2006).

One of the most striking changes observed was the decline in sponge cover, with an expected decrease of 70% immediately following the *Diadema* die-off and remained low throughout all subsequent periods. Some partial recovery throughout the study period was observed by 1-year-post as occasionally observed in other regions of the Caribbean

(Gochfeld et al. 2025). Sponges play a significant role in reef function through water filtration, nutrient cycling, and providing structural complexity (Bell 2008). Their sustained loss suggests long-term disruption to these functions. Our results did not reveal a significant relationship between the change in sponge cover and precedent urchin density, suggesting that other factors could be occurring during our study period. Although the decline may be partly linked to increased algal cover through space competition, shading, or allelopathic effects (McCook et al., 2001; Rasher & Hay 2010), the possibility of confounding factors such as winter swells, storm impacts, or disease cannot be ruled out. Still, the timing of the decline, coupled with the absence of recovery, supports the hypothesis that sponges are vulnerable to the loss of herbivore functional roles.

It is important to note the use of large-area imagery (LAI) in this study, which offers a powerful and relatively novel approach for detecting spatially explicit ecological patterns across benthic communities. LAIs provide a high-resolution, permanent record of reef conditions that can be analyzed for multiple response variables, including coral recruitment, macroalgal expansion, and herbivore (e.g., *Diadema*) distribution within a consistent spatial framework (Burns et al. 2015; Remmers et al. 2023). This enables the repeatable, fine-scale tracking of individual colonies, algal patches, and benthic herbivores over time, which is particularly valuable in studying the ecological processes and regulatory effects following a die-off event. Additionally, LAIs reduce diver subjectivity and increase sampling efficiency over broad spatial extents, which is often a limitation of traditional transect-based methods (Curtis et al. 2023; Remmers et al. 2023). Explicit spatial modeling was beyond the scope of this study and would require further analysis and additional environmental covariates. Instead, LAI's were used to quantify spatial structure within plots in a manner that is robust to irregular sampling and well suited to repeated surveys through time. Additionally, several caveats must be considered when interpreting these estimates. The detectability of *Diadema* in LAIs is influenced by the urchins' position within the reef structure, particularly when individuals are partially obscured in crevices or overhangs. Additionally, this method captures only those urchins visible on the exposed reef surface at the time of image acquisition, potentially underestimating the true density. Urchin density metrics here are estimates that may miss nuanced shifts in urchin demographics or behavior (e.g., diurnal hiding). Despite these limitations, LAIs provide a valuable proxy for *Diadema* density that, when paired with standardized imagery protocols and known limitations, enables robust inference in long-term ecological studies where direct herbivore data are lacking.

Overall, these findings emphasize the lasting impacts of the *Diadema* die-off, particularly the severe and persistent loss of sponge cover. Although algae responded predictably to the decline of herbivory, the lack of recovery in sponges and urchins suggests that ecosystem functions disrupted by the die-off may not readily return to their previous state over the short term. Taken together, these results reinforce the importance of key herbivores in structuring reef communities and highlight how even relatively low *Diadema* densities can contribute substantially to maintaining benthic balance. Their continued absence underscores the potential for long-term ecosystem shifts following widespread mortality events.

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Author contribution This work was conceptualized by NR, WRJ, and ROS. Data collection was carried out by NR, VB, MS, AM, and ROS, and the data were processed by NR, VB, MS, AFG, and SBA. Statistical analyses were conducted by NR, WRJ and ROS. The original draft was written by NR, WRJ and ROS, and all authors contributed to the review and editing of the final manuscript.

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Data Availability Data is provided within the manuscript or supplementary information files and published in Zenodo at https://doi.org/10.5281/zenodo.18500375.

Declarations

Conflict of interest The authors declare no competing interests.

References:

Adam TC, Burkepile D, Ruttenberg B, Paddack M (2015) Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. Mar Ecol Prog Ser 520:1–20. https://doi.org/10.3354/meps11170

Adam TC, Holbrook SJ, Burkepile DE, Speare KE, Brooks AJ, Ladd MC, Shantz AA, Vega Thurber R, Schmitt RJ (2022) Priority effects in coral–macroalgae interactions can drive alternate community paths in the absence of top-down control. Ecology. https://doi.org/10.1002/ecy.3831

Alvarez-Filip L, Gill JA, Dulvy NK (2011) Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. Ecosphere 2(10):art118. https://doi.org/10.1890/ES11-00185.1

Alvarez-Filip L, González-Barrios FJ, Pérez-Cervantes E, Molina-Hernández A, Estrada-Saldívar N (2022) Stony coral tissue loss disease decimated Caribbean coral populations and reshaped reef functionality. Commun Biol 5(1):440. https://doi.org/10.1038/s42003-022-03398-6

Arnold S, Steneck R, Mumby P (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105. https://doi.org/10.3354/meps08724

Barott K, Williams G, Vermeij M, Harris J, Smith J, Rohwer F, Sandin S (2012) Natural history of coral−algae competition across a gradient of human activity in the Line Islands. Mar Ecol Prog Ser 460:1–12. https://doi.org/10.3354/meps09874

Bartoń K (2010) MuMIn: Multi-Model Inference (p. 1.48.11) https://doi.org/10.32614/CRAN.package.MuMIn

Bell JJ (2008) The functional roles of marine sponges. Estuar Coast Shelf Sci 79(3):341–353. https://doi.org/10.1016/j.ecss.2008.05.002

Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc Natl Acad Sci USA 105(42):16201–16206. https://doi.org/10.1073/pnas.0801946105

Burns J, Delparte D, Gates R, Takabayashi M (2015) Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. PeerJ 3:e1077. https://doi.org/10.7717/peerj.1077

Carpenter RC (1988) Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. Proc Natl Acad Sci USA 85(2):511–514. https://doi.org/10.1073/pnas.85.2.511

Carpenter RC (1990) Mass mortality of*Diadema antillarum*. Mar Biol 104(1):67–77. https://doi.org/10.1007/BF01313159

Cramer KL, Donovan MK, Jackson JBC, Greenstein BJ, Korpanty CA, Cook GM, Pandolfi JM (2021) The transformation of Caribbean coral communities since humans. Ecol Evol 11(15):10098–10118. https://doi.org/10.1002/ece3.7808

Curtis JS, Galvan JW, Primo A, Osenberg CW, Stier AC (2023) 3D photogrammetry improves measurement of growth and biodiversity patterns in branching corals. Coral Reefs 42(3):623–627. https://doi.org/10.1007/s00338-023-02367-7

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15(12):1378–1386. https://doi.org/10.1111/j.1461-0248.2012.01861.x

Dudgeon SR, Aronson RB, Bruno JF, Precht WF (2010) Phase shifts and stable states on coral reefs. Mar Ecol Prog Ser 413:201–216

Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc Natl Acad Sci U S A 98(9):5067–5071. https://doi.org/10.1073/pnas.071524598

Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the Caribbean reef coral Monastraea annularis. Ecol Monogr 77(1), 3–18. https://doi.org/10.1890/05-1081

Edmunds P, Riegl B (2020) Urgent need for coral demography in a world where corals are disappearing. Mar Ecol Prog Ser 635:233–242. https://doi.org/10.3354/meps13205

Gochfeld DJ, Brandt ME, Smith TB et al (2025) Site-specific variability in recovery of Caribbean sponge communities following two category-5 hurricanes. Coral Reefs 44:1719–1735. https://doi.org/10.1007/s00338-025-02740-8

Hewson I, Ritchie IT, Evans JS, Altera A, Behringer D, Bowman E, Brandt M, Budd KA, Camacho RA, Cornwell TO, Countway PD, Croquer A, Delgado GA, DeRito C, Duermit-Moreau E, Francis-Floyd R, Gittens S, Henderson L, Hylkema A, Kellogg CA, Kiryu Y, Kitson-Walters KA, Kramer P, Lang JC, Lessios H, Liddy L, Marancik D, Nimrod S, Patterson JT, Pistor M, Romero IC, Sellares-Blasco R, Sevier MLB, Sharp WC, Souza M, Valdez-Trinidad A, van der Laan M, Vilanova-Cuevas B, Villalpando M, Von Hoene SD, Warham M, Wijers T, Williams SM, Work TM, Yanong RP, Zambrano S, Zimmermann A, Breitbart M (2023) A scuticociliate causes mass mortality of *Diadema antillarum* in the Caribbean Sea. Sci Adv 9(16):eadg3200. https://doi.org/10.1126/sciadv.adg3200

Hirota M, Holmgren M, Van Nes EH, Scheffer M (2011) Global resilience of tropical forest and savanna to critical transitions. Science 334(6053):232–235. https://doi.org/10.1126/science.1210657

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265(5178):1547–1551. https://doi.org/10.1126/science.265.5178.1547

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25(11), 633–642. https://doi.org/10.1016/j.tree.2010.07.011

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17(4):360–365. https://doi.org/10.1016/j.cub.2006.12.049

Hylkema A, Kitson-Walters K, Kramer PR, Patterson JT, Roth L, Sevier MLB, Vega-Rodriguez M, Warham MM, Williams SM, Lang JC (2023) The 2022 *Diadema antillarum* die-off event: comparisons with the 1983-1984 mass mortality. Front Mar Sci 9:1067449. https://doi.org/10.3389/fmars.2022.1067449

Lessios HA (2016) The great *Diadema antillarum* die-off: 30 years later. Annu Rev Mar Sci 8(1):267–283. https://doi.org/10.1146/annurev-marine-122414-033857

Lessios HA (1988) Mass mortality of diadema antillarum in the caribbean: what have we learned?

Levitan DR, Edmunds PJ, Levitan KE (2014) What makes a species common? No evidence of density-dependent recruitment or mortality of the sea urchin *Diadema antillarum* after the 1983–1984 mass mortality. Oecologia 175(1):117–128. https://doi.org/10.1007/s00442-013-2871-9

Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D (2021) Performance: an R package for assessment, comparison and testing of statistical models. J Open Source Softw 6(60):3139. https://doi.org/10.21105/joss.03139

Manuel O-S, Williams SM, Weil E, Cruz-Motta JJ (2021) Experimental evaluation of *Diadema antillarum* herbivory effects on benthic community assemblages. J Exp Mar Biol Ecol 541:151566. https://doi.org/10.1016/j.jembe.2021.151566

McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: A review of evidence and mechanisms. Coral Reefs 19(4), 400–417. https://doi.org/10.1007/s003380000129

Mumby PJ, Hedley JD, Zychaluk K, Harborne AR, Blackwell PG (2006) Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: fresh insights on resilience from a simulation model. Ecol Modell 196(1–2):131–148. https://doi.org/10.1016/j.ecolmodel.2005.11.035

Mumby PJ, Steneck RS, Hastings A (2013) Evidence for and against the existence of alternate attractors on coral reefs. Oikos

122(4):481–491. https://doi.org/10.1111/j.1600-0706.2012.00262.x

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Borman T, Carvalho G, Chirico M, De Caceres M, Weedon J (2001) vegan: community ecology package 2.7–1 https://doi.org/10.32614/CRAN.package.vegan

Pante E, Dustan P (2012) Getting to the point: accuracy of point count in monitoring ecosystem change. J Mar Biol 2012:1–7. https://doi.org/10.1155/2012/802875

Petrovic V, Vanoni DJ, Richter AM, Levy TE, Kuester F (2014) Visualizing high resolution three-dimensional and two-dimensional data of cultural heritage sites. Mediterr Archeol Archaeom 14(4):93–100

Pringle RM, Abraham JO, Anderson TM, Coverdale TC, Davies AB, Dutton CL, Gaylard A, Goheen JR, Holdo RM, Hutchinson MC, Kimuyu DM, Long RA, Subalusky AL, Veldhuis MP (2023) Impacts of large herbivores on terrestrial ecosystems. Curr Biol 33(11), R584–R610. https://doi.org/10.1016/j.cub.2023.04.024

Rasher DB, Hay ME (2010) Chemically rich seaweeds poison corals when not controlled by herbivores. Proc Natl Acad Sci 107(21), 9683–9688. https://doi.org/10.1073/pnas.0912095107

Remmers T, Grech A, Roelfsema C, Gordon S, Lechene M, Ferrari R (2023) Close-range underwater photogrammetry for coral reef ecology: a systematic literature review. Coral Reefs. https://doi.org/10.1007/s00338-023-02445-w

Rodríguez-Barreras R, Montañez-Acuña A, Otaño-Cruz A, Ling SD (2018) Apparent stability of a low-density *Diadema antillarum* regime for Puerto Rican coral reefs. ICES J Mar Sci 75(6):2193–2201. https://doi.org/10.1093/icesjms/fsy093

Rogers A, Lorenzen K (2016) Does slow and variable recovery of diadema antillarum on caribbean fore-reefs reflect density-dependent habitat selection. Front Marine Sci. https://doi.org/10.3389/fmars.2016.00063

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29(4):436–459. https://doi.org/10.1017/s0376892902000322

Suka R, Asbury M, Gray AE, Winston M, Oliver T, Thomas A, Couch CS (2019) Processing photomosaic imagery of coral reefs using structure-from-motion standard operating procedures. https://doi.org/10.25923/H2Q8-JV47

Van De Leemput IA, Hughes TP, Van Nes EH, Scheffer M (2016) Multiple feedbacks and the prevalence of alternate stable states on coral reefs. Coral Reefs 35(3):857–865. https://doi.org/10.1007/s00338-016-1439-7

Williams SM (2022) The reduction of harmful algae on Caribbean coral reefs through the reintroduction of a keystone herbivore, the long-spined sea urchin *Diadema antillarum*. Restor Ecol 30(1):e13475. https://doi.org/10.1111/rec.13475

Williams ID, Couch CS, Beijbom O, Oliver TA, Vargas-Angel B, Schumacher BD, Brainard RE (2019) Leveraging automated image analysis tools to transform our capacity to assess status and trends of coral reefs. Front Mar Sci. https://doi.org/10.3389/fmars.2019.00222

Williams SM (2016) A novel approach to the restoration of diadema antillarum on coral reefs in the caribbean.

Young HS, McCauley DJ, Helgen KM, Goheen JR, Otárola-Castillo E, Palmer TM, Pringle RM, Young TP, Dirzo R (2013) Effects of mammalian herbivore declines on plant communities: Observations and experiments in an African savanna. J Ecol 101(4), 1030–1041. https://doi.org/10.1111/1365-2745.12096