Degraded Coral Reefs are Becoming More Resistant to Hurricanes

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Abstract

The frequency and intensity of Atlantic cyclonic storms are projected to increase as climate change warms the ocean [1,2]. These changing disturbance dynamics, paired with simultaneous changes in the condition and composition of Caribbean coral reefs, could be altering reef resilience to storms in unexpected ways. For example, the observed decline of fast-growing, disturbance-sensitive species could promote resistance to and decrease recovery from storms[3,4], increasingly locking reefs into a state dominated by weedy taxa. To test this hypothesis, we combined data from coral reef monitoring studies and historical hurricane records to develop a regional reef-storm interaction database. We found that as the living cover of Caribbean corals declined over the past 40 years, while resistance to storms increased, despite a concurrent increase in cyclonic storm frequency and intensity. Because storms selectively damaged branching coral species and had no measurable effect on the cover of “weedy” corals, reef composition shifted towards greater weedy dominance and reduced ecological function. Additionally, storms accelerated the loss rate of threatened acroporid corals, already in pre-storm decline, suggesting a worrisome synergism with other climate-related disturbances.

Full Text

The U.S. Fourth National Climate Assessment concluded that the ongoing disruption of ocean ecosystems will intensify as ocean warming, acidification, deoxygenation, and other aspects of climate change increase[5]. This is largely due to the growing frequency and intensity of these disturbances. For example, the return time of heat waves on coral reefs decreased from 16 to 6 years between 1985 and 2015[6]. The increased the frequency of mass coral bleaching events is driving reefs into a state of continual recovery, with little chance of returning to a pre-disturbance state.

The severity of oceanic storms is also predicted to increase due to the growing heat content of the ocean surface waters [1,2]. Cyclonic storms are an important source of disturbances to coral reefs[7–10]. High winds and strong waves can fragment or uproot reef organisms or “sand-blast” the tissue off coral skeletons[11.] The ecological consequences of storms include the replacement of storm-sensitive species by weedy competitors, changes in species composition and ecosystem functioning, and a general flattening of reef habitats[7].

Despite the historical importance of storms and the expected increase in storminess, recent studies have reported that the effects of cyclonic storms on coral reefs have become negligible. For example, Edmunds[3] found that the two category 5 hurricanes that struck the reefs around St. John U.S. Virgin Islands in 2017 had no significant effects on living coral cover. Whereas, studies of the impacts of earlier category 5 hurricanes Hattie in Belize (in 1961)[8], Allen in Jamaica (in 1980)[10], and Hugo (1989) in the U.S. Virgin Islands[11] describe catastrophic damage to coral communities. However, the generality of and mechanisms underlying reduced hurricane impacts are unknown.

The purpose of this study was to measure the state-dependent effect of storms on Caribbean reef corals to better understand the causes and implications of changing coral reef resilience to storms. We compiled a coral reef-storm dataset that catalogues the historical record of storm crossings on coral reefs in the greater Caribbean and Gulf of Mexico (Fig. 1A). This database consists of 11,490 quantitative benthic surveys from 3,144 unique reef locations performed between 1970-2017. Survey data was compiled from various coral reef monitoring programs and the literature (Extended Data Table 1) and each survey reported the absolute living coral cover as a percentage of the benthic composition. A subset of the data sources also reported the percent cover of individual coral species (Extended Data Table 1), which we aggregated to determine the percent cover of three ecological functional groups (weedy, competitive, and stress tolerant, see Extended Data Table 2) across 672 unique reef locations. We then combined these coral community data with the tracks of Atlantic storms (tropical storm strength or stronger) sourced from the National Oceanic and Atmospheric Administration (NOAA)'s HURDAT2 dataset[12]. For the 47 years for which we had coral survey data there were 547 storms, 152 of which crossed at least one surveyed reef, resulting in 10,058 unique storm-reef intersections. When coral reef survey data was available for pre- and post- storm years at a site (1 year prior and 1 year post), we quantified the effect of storms on living coral cover and community structure, and their dependency on pre-impact reef state. Specifically, we determined whether pre-storm living coral cover and community composition affected resistance to and recovery from storm damages.

We found that total living coral cover has steadily declined (Fig. 1B) since prior regional assessments[5,6] that suggested coral loss may have plateaued by the late 1990s, at a regional mean of ~16%. However, our results indicate that from 1997 - 2017, the median annual loss rate was ~0.25% per year, with a final year regional mean of 9.5% +/- 0.59% (SE). The more recent regional effects of stony coral tissue loss disease[11], including reports of severe coral loss across the Caribbean[13] suggest further decline since the final year of our study. Despite substantial sub-regional variation (Fig 1.B), coral cover continues to decline even on reefs with relatively high coral cover. The current consensus is that this pattern is driven largely by coral bleaching, disease, and other disturbances, with local stressors including fishing and pollution playing a role at some locations[14].

Our results also indicate that the frequency and intensity of Atlantic storms has increased (Figs. 1C & D, Extended Data Figure 1). Despite more, stronger storms, the immediate effect of storms on total living coral cover decreased markedly between the 1980s/1990s and the 2000s/2010s (Fig. 2A). Storms now have no general effect on total living coral cover. In contrast, in the 1980s, the median short-term loss was -8.5% (for absolute total coral cover, n=10 impacted reefs, maximum loss = 27%). However, Gardner et al.[3] found that Caribbean hurricanes between 1980 and 2001 on average caused a 17% reduction in live coral cover (n=177 impacted reef sites).

One obvious difference is that pre-impact living coral cover has been substantially reduced. Our results indicate that reefs with greater pre-impact cover were less resistant (i.e., reefs lost more cover when other factors are controlled for Extended Data Figure 2, Extended Data Table 3). Numerous other studies have also reported this state-dependent resilience to storms [7,15], and for other large-scale disturbances including disease outbreaks and bleaching events [16–18]. Although this phenomenon is often attributed to simply having more coral to lose, it could also be caused at least in part by the presence of disturbance sensitive species (which historically tended to dominate high-cover reefs[14,19,20]); particularly coral species in the genus *Acropora*. Due to their fast growth and branching or plating morphology, these species are considered competitively dominant over other sessile reef organisms, including other coral species. Once established, acroporid corals can quickly monopolize incoming light and space on the seafloor — two critical resources for many sessile reef organisms.

Only four Caribbean coral species are considered “competitive dominants” [21], three of which are in the genus *Acropora* (*cervicornis, palmata,* and their sterile hybrid *prolifera)*. In U.S. waters, *Acropora* species are also listed under the Endangered Species Act as threatened. These species dominated Caribbean reefs until the early 1980s, when they were nearly extirpated by white band disease — a regional epizootic linked to ocean warming[7,8]. They are particularly sensitive not only to storms and other forms of physical disturbance (due to their morphology), but also to disease, predator outbreaks, and other environmental perturbations[4,8,21]. The result of these vulnerabilities means that *Acropora*-dominated reefs are less resistant to disturbance, despite greater apparent “health”[9,10].

We found that storms drove a change in functional group composition of coral communities on Caribbean reefs (Fig. 2B). In general, acroporid and stress tolerant corals were negatively impacted by storms (average loss for competitive species -0.4% ± 0.12%, Wilcoxon p =0.009; average loss for stress tolerant species -0.66% ± 0.22%, Wilcoxon p = 0.007, also see Extended Data Table 4) causing the relative abundance of coral species categorized as “weedy” to increase.

The changing disturbance regime (e.g., more frequent marine heatwaves, bleaching events, storms, and disease outbreaks) on Caribbean reefs appears to have shifted reef composition into a lower cover but more resistant state. This shift has increased the relative dominance (and in some subregions the absolute cover) of coral species more able to tolerate disturbance, or at least able to quickly recolonize disturbed reefs due to the characteristics of their brooded larvae that stay relatively close to parental populations. Weedy corals grow slower than competitive species, thus post-disturbance recovery and reef accretion could also decline [22]. This compositional shift also degrades other important reef characteristics and functions including vertical reef accretion, surface complexity, and habitat provision [23,24]. In the Caribbean, competitive coral species, and some stress tolerant species in the *Orbicella* genera, disproportionately contribute to increased structural complexity and calcification, whereas many weedy species do not because of their smaller colony sizes and flatter morphologies. The loss of structural complexity is of unique importance due to the established links between complexity and multiple ecosystem services and because changes to complexity are highly influenced by hurricane impacts, compared to other disturbances[25].

Although the immediate effects of storms on coral communities have declined, the longer-term impacts linger for years. Like Gardner et al.[7], we found little evidence of post-storm recovery. Instead, we found a brief period of stasis after the immediate impact of a storm, and then resumption of pre-storm decline (2005). This pattern could be due to delayed disease or coral predator outbreaks triggered by the storm For example, physical damage from tropical storms, such as coral fragmentation and increased sedimentation, may provide more opportunity for contact between pathogens and live coral tissue[26].

When comparing the average rate of change in coral cover between storm-impacted and unimpacted sites, we found that storm-impacted sites still have a negative recovery rate (i.e., continued decline post-storm) in the 2010s while unimpacted sites have a slightly positive rate of change, indicating recovery (Figure 4 below). We know that coral reefs experience a simultaneous myriad of disturbances and stressors, including storms, thermal stress (leading to coral bleaching), disease, and localized impacts from pollution, overfishing, and development. Therefore, it is possible that concurrent or subsequent disturbances or stressors interact with storm impacts to further exacerbate coral cover decline. For example, synergistic interactions between hurricanes and coral disease, in which storm damaged sites have a higher prevalence of coral disease compared to unimpacted sites, has been documented in the Caribbean[27–29]. Thus, the effect of storms on cover, composition, and functioning often continue for a significant period of time after the event.

The contribution of hurricane impacts to coral decline in the Caribbean has decreased over the past few decades; however, localized immediate impacts from storms can still be substantial on reefs with high coral cover or longer time between storm events. Importantly, storms appear to be facilitating a shift towards coral assemblages dominated by weedy species. This shift has eroded reef functionality, but may also increase resistance to other disturbances.

Increasing trends in storm frequency and intensity have important regional implications, not only for natural marine and terrestrial ecosystems and wildlife, but also for people. More, stronger storms will result in increased damage to infrastructure and loss of ecosystem services that humans rely on. For example, recent reports quantified how damage to coral reefs from Hurricanes Irma and Maria in 2017 increased the flood risk to coastal communities in Florida and Puerto Rico. These risks translate to potentially hundreds of millions of dollars in direct and indirect damages to properties and buildings[30]. Like coral communities, any socio-ecological community impacted by hurricanes will likely have decreased time for recovery between storm events under climate change.

Declarations

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Author Contributions

LM and JFB designed and conceptualized the research design and acquired data to perform the study. LM performed the statistical analyses. LM and JFB interpreted the results and wrote the manuscript.

Competing interest declaration

The authors declare no competing interests.

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Methods

Data Availability

The datasets analysed during the current study are available in Laura Mudge's GitHub repository: https://github.com/Lmudge13/Caribbean_Coral_Reef_Hurriane_Impacts. The compiled raw coral cover data set is available from the corresponding author on reasonable request; however, this dataset is not reprinted or publicly available due to license and user agreements from individual databases. All databases included in the coral cover dataset can be accessed using the references provided in Extended Data Table 1.

Coral Survey Data Acquisition

Coral reef benthic survey data was obtained from primary source databases, peer-reviewed literature, and grey literature. Databases included widely-used and publicly available coral reef monitoring programs, such as Reef Check, Reef Life Survey, and the Atlantic and Gulf Rapid Reef Assessment (AGRRA). Primary databases with download date are listed in Extended Data Table 1. This study combined a previous version of a Caribbean coral cover database used for analysis in Selig and Bruno 2010[27] and Schutte et al. 2010[28], with more recent coral survey data from longitudinal studies and monitoring datasets. We relied heavily on data from monitoring programs because they provide large amounts of repeated measurements over long time frames and cover broad spatial scales, both of which are essential for making conclusions regarding regional trends and possibly help mitigate the effects of publication bias[3,29]. Most surveys were not conducted on permanent transects, and GPS coordinates were used to verify the location on the reef for resurveying over time. All monitoring programs collect data on characteristics of the habitat surveyed (e.g. reef zone, such as bank reef or patch reef), which aids in verifying that the same reef area is resurveyed.

Absolute living scleractinian coral cover was measured using quantitative techniques including line transect intercept (in-situ counts along a transect line) and point count (randomized points taken from video transects or photo quadrats). Despite differences in survey methodology and possibly precision and accuracy, the metric of percent cover of the benthos is recognized as a fairly coarse measurement, resulting in negligible differences that are not statistically affected by the method of collection[30, 31, 32, 33, 34]. The data collection methods for obtaining coral species data were similar (AGRRA or modified-AGRRA protocols) and conducted by trained scientists.

Studies were included if they reported a reef site location, survey date (or year), and a measure of absolute percent cover for scleractinian corals. When latitude and longitude coordinates of survey locations were not provided in the reference, we used site location descriptions and maps from the text to identify approximate coordinates using Google Earth, when possible. In addition to manual data entry from primary literature, three tools were used to extract data from pdf resources: the tabulizer package in R[35] was used to extract raw percent cover data from tables, and ImageJ (from previous Bruno lab database only, see Schutte et al., 2010) and/or Web Digitizer[36] was used to extract raw percent cover data from figures. If more than one survey was conducted at the same reef site on any given day, percent coral cover was averaged to produce one value per day/location combination. Coral reef survey locations were considered unique based on the latitude and longitude coordinates provided from the dataset or study. The resulting database includes survey data from 3,144 unique reef locations throughout the Caribbean with 11,490 measurements of coral cover between 1971 and 2017. Approximately 23% of the data came from peer-reviewed literature sources and 77% from coral reef monitoring programs.

Coral Cover by Life History Group

Absolute percent cover of distinct coral species was obtained from three sources, mostly focused in Florida and the US Virgin Islands (Extended Data Table 1, sources with **). Coral species were assigned a life history group (LHG) of either competitive, stress tolerant, or weedy based on classifications made in Darling et al.[37]. These assignments are based on qualities related to species specific growth and reproduction (Supplement Table 2). Coral species not yet assigned to a LHG were labeled as "unclassified". The relative cover for each life history group was calculated by site and year using the calculation:

Building a hurricane and coral reef intersection database

Historical storm track data was downloaded directly from the National Oceanic and Atmospheric Administration (NOAA) Atlantic Hurricane Database (HURDAT2) using the HURDAT package in R[38]. These historical records contain storm track location (latitudinal and longitudinal coordinates), wind speed (knots), low pressure (millibar), status (landfall, hurricane classification), date and time, with variables recorded every 6-hours. Historical track information from the earliest year (1851) to present was used to analyze overall storm patterns in the Atlantic basin. Linear models (ordinary least squares regression) were used to investigate changing trends in the frequency and intensity of tropical storms over time in the Atlantic.

Functional programming in R was used to catalog which hurricanes cross which reef sites in the coral reef survey dataset. Code for these procedures was adapted from Elsner and Jagger[39]. For each reef, I searched for all historical storms occurring within a 100km radius of the reef site coordinates. Storms of any strength were retained within a 35km radius of the reef coordinates, storms of category 3-5 on the Saffir-Simpson scale were further retained between 35-60km, and only category 4 and 5 storms retained between 65-100km. These buffers are based on previously published hurricane path impacts to coral reefs[40,34,6,]. Each observation in the database is a unique reef-storm intersection. Therefore, reef locations appear multiple times in the database, if more than one storm has hit the reef since 1851, and individual storms appear multiple times if they struck multiple coral reef locations along their path.

Historically (1851-2017), approximately 32% of named storms in the Atlantic basin have hit a coral reef location (1,604 named storms, 521 hit a reef). Between 1970-2017, the time period of coral survey sampling, there were 547 storms total, 28% of which crossed over at least one coral reef site, for a total of 10,058 unique site-storm intersections. Out of 3,144 unique coral reef survey sites, 2,754 sites experienced at least one tropical storm since the beginning of storm records in 1851 (87.6% of reefs impacted, 12.4% of reefs unimpacted). Sites that were not impacted were located in the SW Caribbean, along the coast of Panama, Colombia, and Costa Rica.

For each unique reef site, we calculated several measurements pertaining to the disturbance regime of tropical storms, including the total number of storms to ever hit that reef, historical return time (average number of years between storm events), storm dispersion patterns, and the average historical maximum intensity of all storms, weighted by their distance to the reef. All of these variables were calculated from coral-storm intersections that occurred between 1851-2017. The dispersion statistic is used to assess the temporal clustering of hurricanes and has demonstrated ecological impacts on coral reef ecosystems[42,43]. Using previously described methods, we tabulated a count vector (Y) of storm events per reef for each year between 1851-2017. The dispersion statistics (Ψ) is calculated as:

Storm dispersion patterns were characterized as follows[42,43]: Stochastic (random): Ψ (Y) = 0 (i.e. variance = mean); Clustered (over-dispersed): Ψ (Y) > 0 (i.e. variance > mean); Regular (under-dispersed): Ψ (Y) < 0 (i.e. variance < mean).

Control Reefs

A subset of the larger coral cover database was identified to serve as a "control" dataset. This included coral cover data from sites that were either 1) never hit by a storm; 2) had a substantial amount of time (>10 years) between storm events. For sites that had been hit by a storm, coral cover data was only retained for a period of 10 years after a previous storm until the next storm hit. This is to ensure that we were not including potential storm recovery trajectories as part of a control condition. For each reef site, we calculated the annual rate of change in coral cover (CR) to use as a comparison against the rate of change in coral cover at storm-impacted sites[6]. The CR value was also calculated for each Caribbean subregion in order to account for anticipated spatial variation in coral cover and potential local conditions contributing to coral decline.

Quantifying Resilience

Resistance

Coral resistance to tropical storm damage was measured as the absolute change in coral cover from initial conditions (one year prior to a storm) and one-year post-storm. Paired Wilcoxon tests were used to quantify differences in cover before and after each individual storm event at each reef (i.e. each site-storm combination is one observation for this test). A Kruskal-Wallis test was used to test the hypothesis that coral resistance is greater (meaning less coral loss from storms) in more recent decades.

Recovery

Temporal patterns in coral recovery were quantified in two ways: as (1) the relative change in coral cover at any year pre- or post-storm, relative to coral cover in the year preceding a storm, here referred to as the initial conditions; and (2) as the annual rate of change in absolute coral cover (CR), post-storm[44,36,6].

(1) Relative recovery = % cover at year relative to storm - % cover before impact

(2) Annual rate of change in coral cover (CR) = (pca-pcb)/d

Quantifying the relative change in coral cover for years both before and after a storm event allows us to compare the impact of storms on pre-disturbance trends. First, I used regression models to evaluate the trend in relative recovery for the time periods pre- and post-storm. Upon visual review of linear regression (using ordinary least squares models), it became apparent that one linear relationship did not persist throughout the time period of recovery, but rather multiple piecewise relationships might exist. We used the segmented package in R to estimate the appropriate breakpoints for the regressions[45]. We then compared the slopes in the piecewise regressions for several time periods pre- and post- storm to describe patterns of recovery. Next, we quantified the annual rate of change in coral cover (CR) after a storm event. CR is measured over each individual storm event time series, in which pca is the percent cover at the end of the time series, pcb is the coral cover immediately after a storm (post one-year), and d is the duration of the time series, calculated as the number of years between pcb and pca. If two or more storms occurred in the same year/site, the CR time series was kept for the stronger storm and/or later storm. Resistance and recovery were quantified for both absolute coral percent cover (all species) and the relative abundances of coral life history groups.

Linear mixed models were used to quantify the effects of a variety of disturbance characteristics on coral resistance and recovery. Predictors included a mix of event specific characteristics and disturbance regime characteristics (Extended Data Table 3). All predictors were treated as fixed effects, except for reef location, which was treated as a random effect to account for variation amongst individual reef sites. Prior to modeling, raw data were analyzed for normality, heteroscedasticity, outliers, and collinearity via pairs plots and variance inflation factors (VIF). Predictors with a VIF > 2 were removed from the model. Historical return time and the historical number of storms were collinear and had high VIF and for each model, whichever variable had the higher VIF was removed. In the resistance models for coral life history groups, storm distance was also removed due to high collinearity with wind speed and high VIF. Response variables had a non-normal distribution and included both zeros and negative values, so a cube-root transformed was performed prior to modeling. All continuous fixed effects were scaled prior to modeling. Model residuals were also evaluated to meet assumptions of normality and homoscedasticity. Models were run using the lme4 package[46] in R. All analyses were conducted in R version 3.6.1.

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Figures

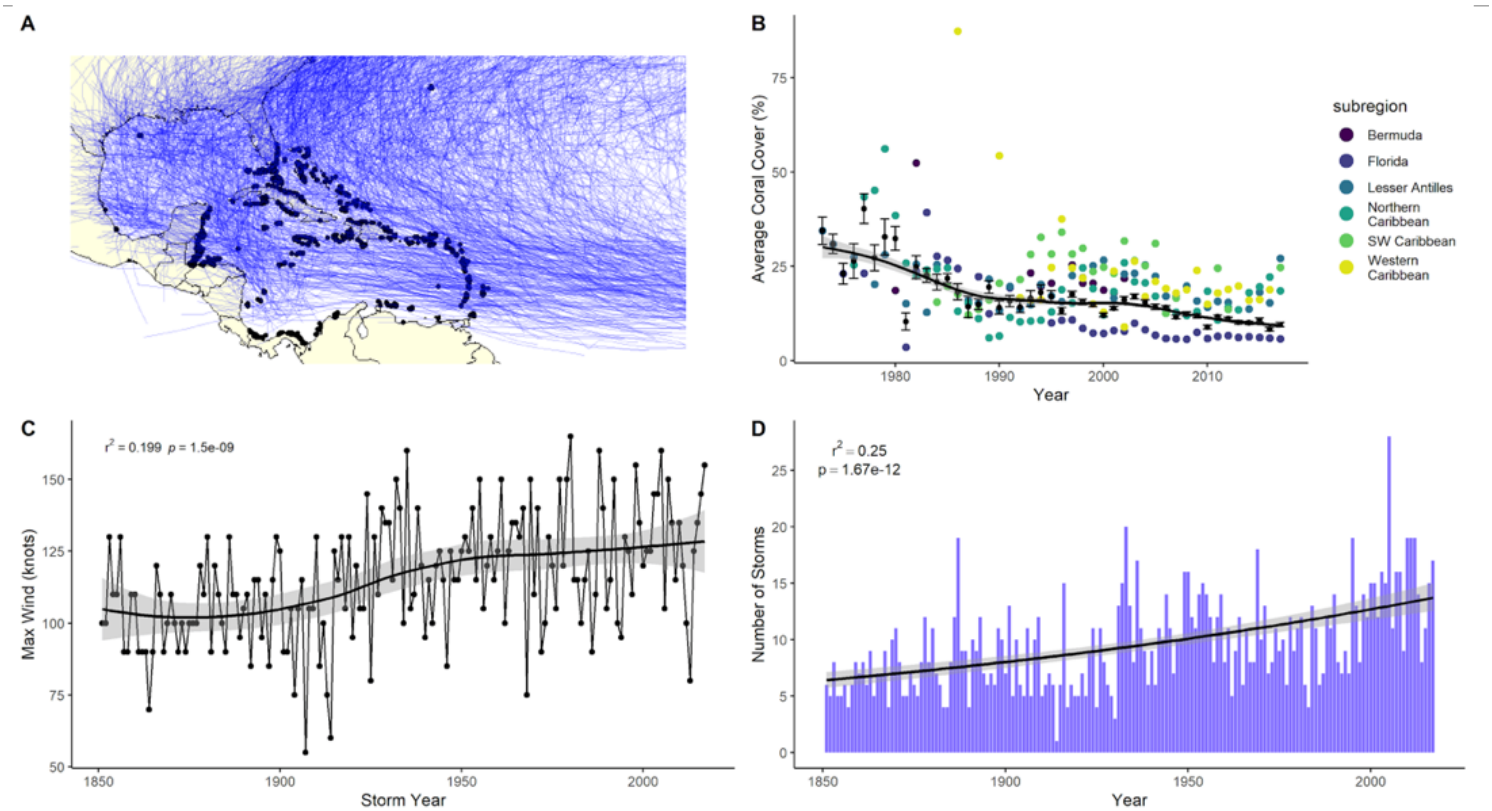

Figure 1

A) Atlantic storm tracks from 1851-2017. Storm tracks are represented by blue lines and unique coral reef survey locations by black points. B) Caribbean coral cover trends 1970-2017. Colored points represent subregional annual averages in scleractinian coral percent cover. Black points represent basin wide annual averages in percent cover (+/- standard error), C) Increase in the maximum wind recorded for any Atlantic storm in a year; D) Increase in Atlantic storm frequency.

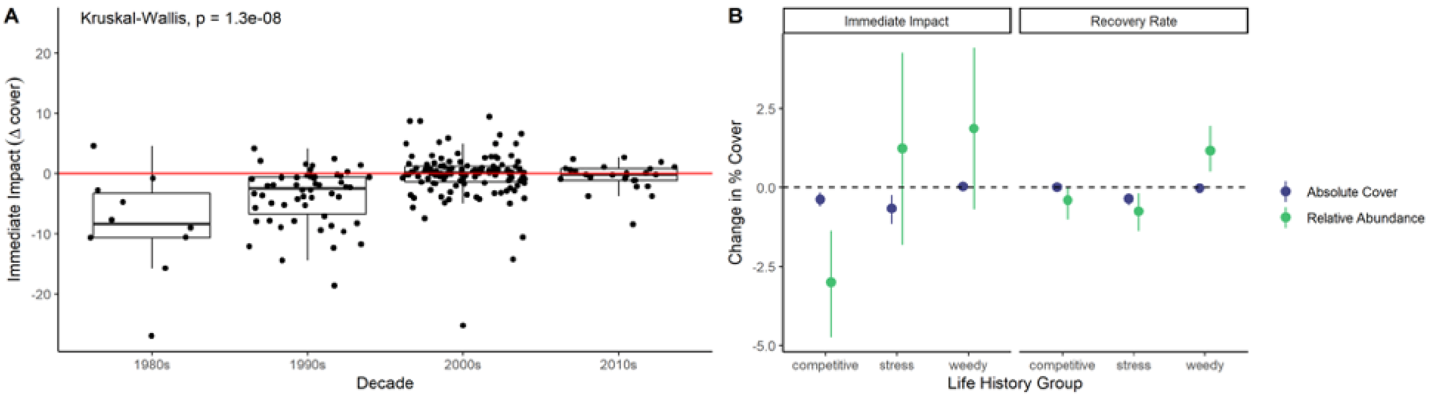

Figure 2

A) Temporal trends in immediate storm impacts on total coral percent cover. Each data point represents one storm/reef event; B) Post-storm immediate impact and recovery rates (annual rate of change) for different coral life history groups. Points represent average values ± non-parametric bootstrapped confidence limits.

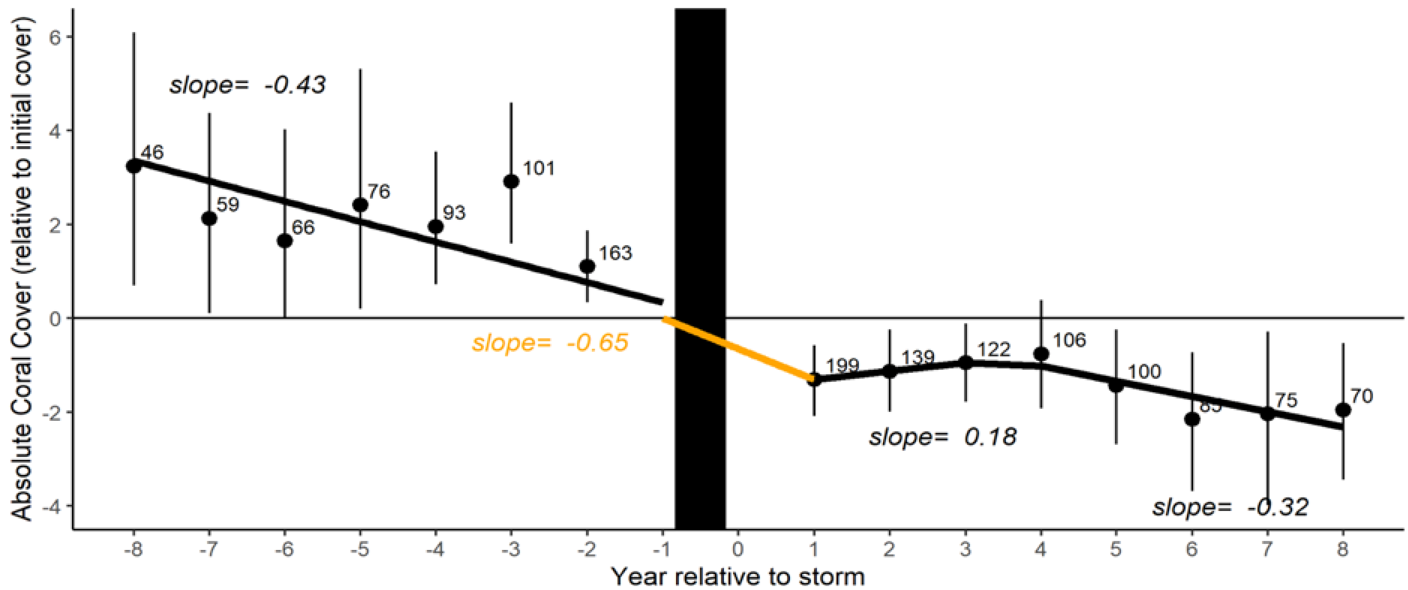

Figure 3

Average yearly change in coral cover, relative to year of impact. The vertical black bar represents a storm event on a reef. Black dots are the Caribbean-wide average change in coral cover for any year pre/post storm (±bootstrapped confidence intervals), relative to initial cover (percent cover at one year prior to storm). Numbers represent sample sizes for averages. Lines represent the slope of change in coral cover pre- and post- storm, with the orange line representing immediate impact.

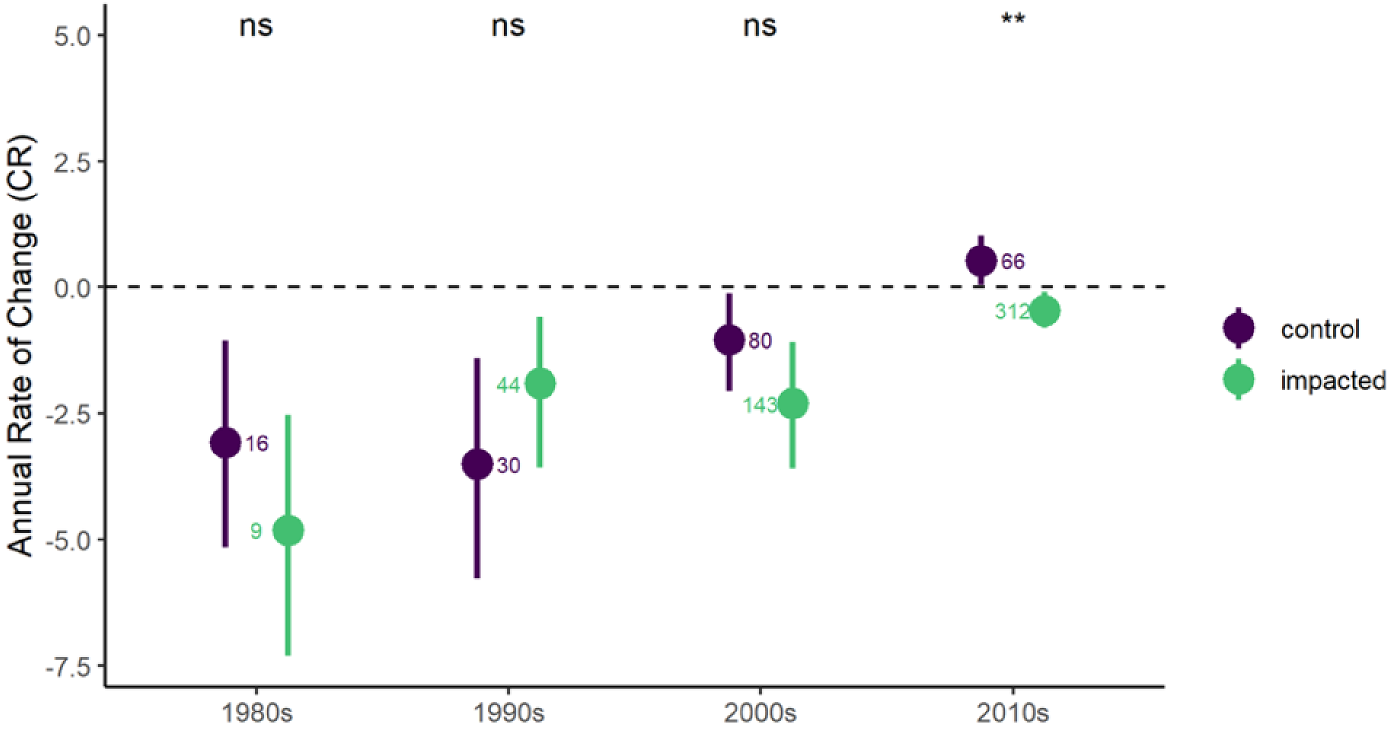

Figure 4

Annual rate of change in absolute coral cover between control and storm-impacted sites, by decade. Points represent Caribbean wide-averages (±bootstrapped confidence intervals)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ExtendedData.docx