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Article

Keywords: coral reefs, emergent disease, Caribbean

Posted Date: November 4th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-734716/v1>

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An emerging coral disease outbreak decimated Caribbean coral populations and reshaped reef functionality

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Abstract

Diseases are major drivers of the deterioration of coral reefs, linked to major declines in coral abundance, reef functionality, and reef-related ecosystem services¹⁻³. An outbreak of a new disease is currently rampaging through the populations of the remaining reef-building corals across the Caribbean region. The outbreak was first reported in Florida in 2014 and reached the northern Mesoamerican reef by summer 2018, where it spread across the ~ 450-km reef system only in a few months⁴. Rapid infection was generalized across all sites and mortality rates ranged from 94% to < 10% among the 21 afflicted coral species. This single event further modified the coral communities across the region by increasing the relative dominance of weedy corals and reducing reef functionality, both in terms of functional diversity and calcium carbonate production. This emergent disease is likely to become the most lethal disturbance ever recorded in the Caribbean, and it will likely result in the onset of a new functional regime where key reef-building and complex branching acroporids (a genus apparently unaffected) will once again become conspicuous structural features in reef systems with yet even lower levels of physical functionality.

Main

Disease outbreaks are often associated with mass mortality events that can rapidly and drastically reduce populations over short periods of time⁵⁻⁷. When these events affect foundation species, the consequences exceed the species level and alter the structure and functioning of the entire ecosystem^{8,9}. In the marine realm, Caribbean coral reefs offer some of the best examples of such catastrophic events. This region is a well-known hot spot for diseases^{1,10} and many have decimated the populations of primary reef-builders, resulting in devastating changes to the spatial heterogeneity of the reefscape, its capacity to provide ecosystem services, and the ability to track sea-level rise^{1,11}. In the late 1970s, a region-wide outbreak of white-band disease led to population losses of nearly 80% of the major reef-building corals *Acropora palmata* and *A. cervicornis*¹², resulting in a notable reduction in reef functionality (e.g., ¹³⁻¹⁵). Since then, multiple disease outbreaks have nearly decimated the populations of many other key reef-building corals^{1,2}. Moreover, there is an ever-increasing risk of diseases to further impact the stability of reef ecosystems, as the frequency and intensity of disease outbreaks are often related to rapidly increasing human-induced pressures, such as rising sea temperatures, decreased water quality, and nutrient enrichment¹⁶⁻²⁰.

In 2014, the south-eastern Florida sub-region saw the onset of a new deadly coral disease, known as Stony Coral Tissue Loss Disease (SCTLD;²¹). It had spread across the Caribbean with reports

of SCTLD in the Western Caribbean, Bahamas, Puerto Rico, and the US Virgin Islands and recent reports in the Lesser and Greater Antilles²². The sources of transmission and specific causative agents are not yet fully understood, although recent evidence suggests that the disease is transmitted through seawater and that bacteria consortium taxa are involved in disease progression^{23–25}. Most of the evidence of the devastating effects of SCTLD comes from Florida and Mexico^{4,26}, yet similar outcomes have been reported elsewhere in the region. SCTLD affects nearly 30 different coral species and is highly virulent, spreading rapidly within reef systems^{27,28}. Highly susceptible species (e.g., *Meandrina meandrites* and *Dendrogyra cylindrus*) are rapidly infected and can die within weeks^{21,29}. Coral density and composition and environmental conditions, including nutrient concentrations and turbidity, likely influence disease prevalence and progression^{4,21,26,30,31}. However, high water temperatures do not appear to directly influence SCTLD prevalence or virulence^{4,23,27,28}.

SCTLD now threatens many coral species that serve as important reef-builders and habitat providers in most of today's Caribbean reefs³², which raises the question of whether post-SCTLD coral assemblages will be able to maintain key geo-ecological functions, such as reef framework production, sediment generation, the maintenance of reef habitat complexity, and the capacity for coral reef growth that is needed to track future sea level increases¹¹. These functions largely rely on the capacity of coral assemblages to create complex three-dimensional structures by means of calcium carbonate precipitation - here defined as the reef physical functionality. This is particularly relevant in the Caribbean, as lower levels of functional diversity are present compared to those in other regions (e.g., the Great Barrier Reef). Moreover, many key functional attributes of reef-building corals are redundant and only a few species determine the physical functionality of the coral community^{33,34}. Here, we used extensive pre- and post-SCTLD data along a 450-km reef track in the Mexican Caribbean to examine the regional effects of this emerging threat and estimated the consequences of catastrophic coral die-off on the functional integrity of Caribbean reefs. We show that coral mortality was widespread and corals with intimate phylogenetic (i.e., families) and functional trait relationships were disproportionately affected by SCTLD, favoring the hyper-domination of coral species that are mediocre contributors to reef functionality.

Results and Discussion

In only a few months, SCTLD spread across hundreds of kilometers and triggered an unprecedented loss of corals (Figs. 1, 2). Out of the 29,095 colonies surveyed between July 2018 and January 2020, 17% were already dead with signs of recent mortality (e.g., bare skeletons or covered by a thin layer of filamentous algae; Fig. 1) and an additional 10% were afflicted by the disease. However, susceptibility and mortality varied greatly between species. Twenty-five of the 48 recorded species were affected by the disease, with disproportionate effects observed in a single morpho-functional group largely defined by massive species with mid-to-large sizes, dense skeletons, low growth rates, and broadcasting sexual reproduction (Fig. 1). Species from the Meandrinadae and Mussidae families were the most severely affected. In particular, *Dendrogyra cylindrus* and *Meandrina spp.* experienced disease prevalence and population losses greater than 80% (Fig. 1). A temporal comparison of community compositions with pre- and post-outbreak data revealed that less conspicuous species, such as *Dichocoenia stokesii* or those within the Mussinae subfamily, were noticeably less abundant after the outbreak (Fig. S1), indicating that these species were more severely affected than what our post-outbreak surveys suggested. This is likely because the skeletons of the small and encrusting species killed by the disease were rapidly covered by algae or sediment, rendering them inaccessible during post-outbreak surveys.

Figure 1. Morpho-functional groups of Caribbean corals and their susceptibility to Stony Coral Tissue Loss Disease (SCTLD). a) Hierarchical clustering dendrogram based on a Gower dissimilarity analysis and heat map representation of functional traits (numerical values from 1 to 5 correspond to the categories listed in Table S1). b) Prevalence of SCTLD for coral species across 101 reef sites in the Mexican Caribbean (n = number of colonies). We included coral colonies with total mortality whose deaths could be attributable to SCTLD. b) The shaded area corresponds to the prevalence of SCTLD for each morpho-functional group in a). The asterisk (*) indicates species with > 10% disease prevalence (these were considered highly susceptible species, see Methods for more details). c) *Pseudodiploria strigosa* colony with the characteristic lesions produced by SCTLD in Puerto Morelos (July 2018). d) *Dendrogyra cylindrus* colony afflicted with SCTLD showing extensive recent mortality in Sian Ka'an (September 2018). e) A recently deceased colony of *Meandrina* sp. (covered by a homogenous, thin layer of filamentous algae) in Akumal (September 2018).

The affection of the SCTLD outbreak was consistent across the geography and environmental gradients. The only region not afflicted by the disease outbreak (at least until the last survey in February 2021) was Banco Chinchorro (Fig. 2). This is an isolated offshore bank with restricted access that is separated from the mainland by a deep-water channel in which the strong northward Yucatan Current likely acts as a physical barrier to biological connectivity and land-based perturbations. Across all surveyed sites, disease prevalence (considering both diseased and dead colonies) in highly susceptible species showed no statistical differences with regard to depth, reef zone, structural complexity, wind exposure, or coral density (Table S1; Fig. S1), suggesting that the main drivers of contagiousness are largely controlled by the capacity of the pathogen(s) to be transported in the water column within and between reef sites. However, we did find a positive relationship between disease prevalence and the threat of coastal development and the age of marine protected areas (MPAs; Table S1; Fig. S2), although these effects were driven by the reef sites of Banco Chinchorro and did not hold when the reefs of this offshore-bank were removed from the analyses (Table S2; Fig. S3), despite many reef sites

in the central Mexican Caribbean are also found in areas with small human populations and have been under official protection since the 1980s (Fig. 2).

Our results contrast with those of previous studies that have identified site-level differences in the effects of SCTLD related to reef exposure, the distance from the coast, and community composition^{27,30}. This might be partly explained by the rapidness of the spread of the disease and the high mortality rate once infected^{4,21,32}. In addition, our surveys were conducted at different stages of disease progression. In some sites, the disease was still evident in many colonies of susceptible species (i.e., epidemic stage), while in others, the mortality of highly susceptible coral species was widespread and the disease was also present in less susceptible species (i.e., endemic stage;⁵²). Therefore, our broad-scale field surveys did not allow for definitive assessments of the roles of environmental or ecological predictors on the rapid regional coral mortality that was observed. However, a critical pattern depicted by our models indicated that when the disease reaches a site, coral mortality and the disappearance of key reef-building species will most likely occur regardless of local-scale differences, which drives regional changes in the structure and functions of reef communities.

Figure 2. Prevalence of Stony Coral Tissue Loss Disease (SCTLD) in highly susceptible species in the Mexican Caribbean. a) White plague-type disease prevalence in species highly susceptible to SCTLD in 35 sites surveyed before the outbreak of the disease (2016 and 2017). b) SCTLD prevalence (i.e., diseased and recently deceased colonies) in highly susceptible species during or after the SCTLD outbreak (2018 and 2020). In a) and b), the circles represent the locations of the reefs that were sampled before and after the outbreak. The triangles represent the sites that were only surveyed during or after the outbreak. The size of the figure indicates the percentage of healthy colonies from highly susceptible species from the total number of surveyed colonies at each site and time period (including all coral species). The insets in a) and b) represent the distributions of the densities of live coral colonies of highly susceptible species across all surveyed sites for each period. The data points represent each surveyed site, and the box plots depict the median (horizontal line), the first and third quartiles (box height), and 95th percentiles (whiskers). The shaded area (violin plot) depicts the kernel density showing the probability of the data at different values. Highly susceptible species are those with more than 10% disease prevalence (see Methods and Fig. 1).

Abrupt coral die-off radically reduced the abundance of species and the traits that support the physical functionality of coral reefs. Most of the reefs shifted further away from the dominance of reef-building species that are key providers of three-dimensionality to depauperate assemblages dominated by taxa with simpler morphological attributes and slower growth rates. The results of the Similarity Percentage (SIMPER) analysis show that even before the outbreak, most coral reefs in the region were already largely dominated by encrusting and sub-massive agaricids and *Porites astreoides*, which are weedy coral species that accounted for 63.33% and 71.83% of the similarity between sites before the outbreak and after the coral die-off, respectively (Fig. S4). The relative increase in the abundance of these two groups accounted for 50.42% of the dissimilarity between periods (pre- and post-outbreak), while decreases of highly susceptible species accounted for only 13.06% of the dissimilarity, as many of these were either uncommon or rare species (Table S3).

Given that the species that suffered the most severe losses share key life-history traits (Fig. 1), the functional space of the coral assemblages was considerably reduced at regional scales after the outbreak. A before-after analysis at species and family levels and the multi-dimensional trait space of the coral assemblages weighted by the absolute abundance of taxa contributing to each trait revealed a drastic transformation towards more homogenous assemblages as determined by taxonomic and functional trait data, with a notorious lack of contributions from the most severely afflicted species during the post-outbreak period (Fig. 3a-c). These emerging novel assemblages were remarkably characterized by the presence of acroporid corals and their life-history traits (Fig. 3a-c) despite their low abundance across surveyed sites (Table S3). Not surprisingly, composition changes resulted in significant losses of functional richness ($t = 2.67$, $df = 46.04$, $p = 0.01$) and functional evenness ($t = 3.81$, $df = 65.54$, $p > 0.01$) in the coral assemblages (Fig. 3 d,e) despite an apparent increase in species richness ($t = -2.3562$, $df = 65.187$, $p = 0.02148$) that resulted from increased survey effort during the post-outbreak period (Fig. S5; Table S4; see methods). Ultimately, these losses were reflected in a marked reduction of the capacity of coral communities to accumulate calcium carbonates (regional mean $\pm$ SE; 4.60 ± 0.77 G = Kg $\text{CaCO}_3 \text{ m}^2 \text{ yr}^{-1}$ before the outbreak to 3.27 ± 0.53 G after the outbreak; $t = -3.005$, $df = 34$, $p = 0.004$) that was largely driven by the loss of highly susceptible species (3.04 ± 0.62 G pre-outbreak to 1.91 ± 0.34 G post-outbreak).

Figure 3. Shifts in coral community composition and functioning following the SCTLD outbreak. a–c) Principal component biplots of the shifts in the coral assemblages in 35 reef sites along the Mexican Caribbean between the pre- (blue) and post-outbreak (red) periods in a) coral assemblages, b) family assemblages, and c) functional traits based on community weighted means (CWM). The points in a–c) represent the reef sites for each period. Vectors represent the absolute contributions of families, species, and traits. The colored ellipses represent the 95% confidence intervals around the weighted average of the site scores for each period. d–f) Box plots of the functional shifts between the pre- (blue) and post-outbreak (red) periods in the same reef sites with regard to d) functional richness, e) functional evenness, and f) coral community calcification (Kg CaCO₃ m² yr⁻¹). The points in d–f) represent each surveyed reef site and box plots represent the median (horizontal line), first and third quartiles (box height), and the minimum and maximum values (whiskers; excluding outliers). Species key in b): Acer: *Acropora cervicornis*; AGAR_enc: *Agaricia* encrusting; Apal: *Acropora palmata*; Aten: *Agaricia tenuifolia*; Cnat: *Colpophyllia natans*; Dcyl: *Dendrogyra cylindrus*; Dlaby: *Diploria labyrinthiformis*; Dsto: *Dichocoenia stokesii*; Efav: *Eusmilia fastigiata*; Ffra: *Favia fragum*; Hcuc: *Helioseris cucullata*; ISOP: *Isophyllia* spp; MADR: *Madracis* spp; Mang: *Mussa angulosa*; Mcav: *Montastraea cavernosa*; MEAN: *Meandrina* spp; MYCE: *Mycetophyllia* spp; Oann: *Orbicella annularis*; Ofav: *Orbicella faveolata*; Ofra: *Orbicella franksi*; P_dig: *Branching Porites*; Past: *Porites astreoides*; Pcli: *Pseudodiploria clivosa*; Pstr: *Pseudodiploria strigosa*; SCOL: *Scolymia* spp; Sint: *Stephanocoenia intersepta*; Srad: *Siderastrea radicans*; Ssid: *Siderastrea siderea*.

The ecology and physical functionality of coral assemblages in the Caribbean were undergoing severe ecological changes prior to the SCTLD outbreak. Chronic and acute disturbances had progressively driven a decline in the abundance of the main reef-building corals accompanied by a concomitant increase in the relative or absolute abundance of opportunistic corals (Fig. 4). The pre-SCTLD communities were described as ‘shifted’ coral assemblages, and the contributions of formerly dominant acroporids were often negligible given their reduced abundance, whereas large massive species remained and contributed the most to ecosystem structure and functionality (Fig. 4; ^{33,35–37}). However, the resulting wide-spread coral mortality described here was dictated by the vulnerability of species to SCTLD, and thus caused non-random changes in community structure that further and radically affected the functional integrity of the coral communities.

The morpho-functional groups comprised of large and massive species were the most afflicted by the SCTLD outbreak (Fig. 1), whereas the species mildly affected by the disease showed relative increases in abundance. The post-SCTLD coral communities are now represented by a hyperdomination of opportunistic corals, although this remarkably seems to be accompanied by an apparent resurgence of acroporids as key functional elements (Figs. 3a-c, 4). However, the increase of acroporids is primarily an artefact of the drastic reductions in the relative contributions of many other species due to SCTLD (Fig. 4). Only a minor proportion of the increase in the contributions of acroporids may be explained by population recovery or re-sheeting growth over relict reef structures^{38–40}. However, these increases are primarily artefacts of the drastic reductions in the relative contributions of many other species (Fig. 4). In fact, the acroporid populations have remained low compared with their historical estimations^{14,15}, as these species have low biological connectivity, reduced genetic diversity, impaired recovery abilities, and high vulnerability to regional and global stressors^{15,41}. Although it is encouraging that acroporid populations have remained relatively unchanged after the SCTLD outbreak, it is unlikely that these species will significantly improve the structure and dynamics of rapidly changing Caribbean coral assemblages given current conditions.

Figure 4. Schematic of the long-term trajectory of the physical functionality of Caribbean reefs. The stacked plot represents the functional contributions of four coral groups over time. The pie charts illustrate the proportional contributions of each coral group during three different periods. *Acropora* spp. and *Orbicella* spp. contain all the species for each of these genera and are illustrated as a single group, as they are the main reef-building corals in the Caribbean. The group of massive corals includes important reef framework builders from the *Diploria*, *Pseudodiploria*, *Colpophyllia*, *Montastraea*, and *Dendrogyra* genera (many of which were severely affected by SCTLD and were included in the second morpho-functional group from the top in Fig. 1A). The other group includes all other coral species, which are largely classified as weedy, submassive, or foliose-digitate corals (included in the third and fourth morpho-functional groups from the top in Fig. 1A) for which little evidence of declines exists. The black arrows indicate major sources of coral decline widely recognized in the literature. White-band disease resulted in severe population declines of acroporids¹². The white-pox epidemic has infected many of the remaining colonies of this genus since the 1990s⁴². Other coral syndromes (e.g., white plague and Caribbean yellow band) that mainly affect *Orbicella* and other massive species have increased in frequency and virulence over the last three decades (e.g.,⁴³). Coral mortality has also continued to increase in the Caribbean and is associated with warm-water bleaching events and other local-scale anthropogenic impacts^{15,44,45}. The grey-dashed arrows indicate that the source of stress remains, although the effects on widespread coral mortality are unclear.

The large-scale loss of the functionally important corals defined radical shifts in reef conditions and dynamics, exacerbating further losses of ecological integrity along the entire reef track. Overall, the outcomes of coral die-off from the SCTLD outbreak will compromise key geo-ecological functions, such as reef framework production, sediment generation, the maintenance of reef habitat complexity, and the capacity for coral reef growth that is needed to track future increases in sea level^{11,46}. In this study, we observed a nearly 30% reduction in the capacity of coral communities to produce calcium carbonate. This is alarming because levels of community calcification were quite low when compared to those of historical records or those in other regions of the world prior to the impacts of SCTLD⁴⁶. While key processes related to reef construction come to a halt with coral mortality, the structures provided by the calcium carbonate skeletons remain in place for several years after the living tissues die. Thus, key functional aspects associated with the tridimensionality of the system, such as habitat provision or the modulation of water energy, will remain for a period after the death of the corals¹¹.

In the absence of recovery, the ultimate consequences of coral mortality will thus be modulated by destructive forces like bioerosion or the biogenic dissolution of reef structures⁴⁷. Although erosion rates appear to have declined in the Caribbean, erosion is becoming the primary factor controlling the carbonate budgets^{48,49}. This is particularly relevant as both bioerosion rates and skeletal dissolution are thought to become pervasive when the water chemistry changes or the temperatures increase^{50,51}. Our understanding of how the increased availability of substrate for bioeroders will interact with rapid environmental changes remains limited. However, if the ultimate objective is preserving coral reef functioning and services, it may be necessary to focus on replenishing and favoring the recovery of coral communities while improving our understanding of how to control and modulate the destructive forces operating within coral reefs.

The widespread coral die-off associated with SCTLD has affected the populations of many important reef-building species. In the Caribbean, the wide-spread consequences of this outbreak are yet to be known. However, the rapid movement of the disease across the region²² and the overlapping distribution ranges of most species within the Greater Caribbean region^{34,53}, suggest that the outbreak will affect the entire region as has occurred with previous disease outbreaks^{1,10}. Therefore, some species will rapidly be at a clear risk of extinction across their distribution ranges (e.g., *D. cylindrus*; Fig. 1a; ²⁹), while other susceptible species that underwent comparatively lower declines (30–70%; e.g., brain corals) will also have compromised abilities to overcome future sources of stress. For example, the evident declines in the populations of species belonging to the Meandrinidae and Mussidae families could reduce their levels of genetic diversity (e.g., ⁵⁴), putting these species at risk of bottleneck events that would limit their ability to cope with environmental change⁵⁵. In addition, the levels of isolation of the remaining colonies will reduce or hinder the capacity for sexual reproduction (e.g., allele effect) and genetic recombination, further diminishing the abilities of populations to adapt to rapidly changing conditions⁵⁶. Moreover, many afflicted species are slow growing (Fig. 1, Table S5), and the replacement of dead corals will undoubtedly take decades while many acute and chronic stressors operate on smaller temporal scales⁵⁷. This is particularly relevant given that corals weakened by SCTLD are likely to be more susceptible to subsequent disease outbreaks and to other threats like bleaching.

One key question for the coming years is whether populations of highly afflicted species will be able to recover and sustain key geo-ecological functions. To date, we have little evidence in this regard. Empirical observations during our surveys have shown that small (< 5 cm) *Meandrina*, *Diploria*, or *Pseudodiploria* corals have apparently remained unaffected by SCTLD, even in sites that underwent severe losses in adult populations (Fig. S6). Furthermore, recent evidence shows that coral colonies with evident lesions associated with SCTLD can spawn and produce viable gametes⁵⁸. However, the replacement of dead corals through larval recruitment or the growth of small juveniles will take several years given low larval survival and the slow growth rates of most species^{59,60}. In addition, coral recruitment (i.e., the successful settlement of coral larvae) and subsequent survival will largely depend on suitable ecological conditions, such as low densities of harmful fleshy macroalgae⁶¹. Unfortunately,

in our study region and elsewhere in the Caribbean, there is extensive evidence indicating that macroalgae cover is progressively becoming a dominant component of benthic reef communities^{62,63}. It is likely that macroalgae will rapidly overtake the free space left by recently deceased corals (e.g.,²⁸), hindering coral recovery by impeding the settlement of new recruits and reducing the likelihood of colonies that were able to slow or halt disease progression to recolonize their own structures or neighboring substrates (e.g.,^{31,64}). Natural processes might therefore be insufficient to restore the severe population losses of many coral species due to the SCTLD outbreak. Rather, it is likely that human interventions in the form of rescuing colonies of vulnerable species, preserving their genetic material, and implementing restoration efforts will be needed to facilitate recovery and prevent the region-wide extinction of some species (e.g.,²⁹). We believe, however, that these actions will only succeed if they are accompanied by stringent controls that take into consideration climate change, coastal development, and wastewater treatment to improve local conditions and ecosystem resilience.

Methods

Field surveys and SCTLD prevalence

To assess the spread and impacts of SCTLD, extensive surveys were conducted across the Mexican Caribbean between July 2018 and January 2020 (post-outbreak period). In total, 101 sites were surveyed (82 fore-reefs, 19 back-reefs, and four reef-crests) in depths ranging from 1–24 m (Fig. 2). Thirty-five of these sites were also surveyed in 2016 and 2017 (pre-outbreak period) as part of a separate effort⁴⁵ and were used to investigate the ecological and functional consequences of the SCTLD outbreak. These 35 resampled sites are also distributed across the Mexican Caribbean (Fig. 2) and cover similar habitats and depth gradients (thirty reef sites are fore-reefs and five are back-reefs). For the pre-outbreak period, white plague-type disease prevalence is reported as there were no reports of SCTLD for that period.

All sites were surveyed using the Atlantic and Gulf Rapid Reef Assessment protocol⁶⁵. At each site, coral assemblages were surveyed in 10 x 1 m transects. For the pre-outbreak period, 1–7 transects (mean = 2.8; SD = 1.4) were evaluated in each site. For the post-outbreak period, we considerably increased the effort to ensure the representation of uncommon and rare species that we knew were affected by SCTLD, and between 3–23 transects (mean = 8; SD = 3.71) were conducted in each site. The following information was recorded for each coral colony within each transect: species name, colony size (maximum diameter, diameter perpendicular to the maximum diameter, and height), bleaching percentage, mortality percentage (new, transition, and old), and the presence of SCTLD or other diseases⁶⁵. For this study, we also recorded colonies with 100% mortality that could be attributed to SCTLD (i.e., recent or transient mortality was still evident; e.g., Fig. 1e).

We focused on exploring the prevalence and geographical and temporal trends of the most ‘highly susceptible species,’ which were species with more than 10% disease prevalence (considering diseased and recently deceased colonies). For this, we used the information from the 101 sites surveyed during the post-outbreak period to calculate SCTLD prevalence for each site and coral species. Although *S. siderea* showed different signs of infection (termed white-blotch syndrome in some studies; Gintert et al., 2019), we considered this species to be affected by SCTLD due to the timing of the onset of signs and the disease progression being similar to what we observed with other species. In addition, to generate an overview of the outbreak status of the Mexican Caribbean, we calculated SCTLD prevalence for each site and each period using only highly susceptible species.

Effect of environmental and anthropogenic covariates on SCTLD prevalence

We model the percentage of afflicted colonies as a function of coral colony density (prior to the impacts of the disease), reef structural complexity, reef zonation, depth, and the degree of exposure to dominant winds. In addition, we evaluated the influence from land-based human activities using the Coastal Development level (World Resources Institute database, ⁶⁶) and protection status using MPA age. These variables were selected based on their importance to coral reef health and the known susceptibility of coral assemblages to disturbance (^{45,67}, see Table S4 for details), depending on the availability of information for the 101 sites. Water temperature or thermal stress were not included, as remote sensing data do not capture local variation at the necessary resolution (4 km; ⁶⁸). Furthermore, previous studies have shown that temperature is a poor predictor of the spatial variation in coral reef conditions in this ecoregion⁶⁹ and that high water temperatures do not affect SCTLD prevalence or virulence^{4,23,27,28}. We used generalized linear models (GLMs) with the *glm* function in R⁷⁰, setting the percentage of afflicted colonies as the response variable and the aforementioned factors as the predictive variables. A gaussian distribution with an identity link function was adopted as the goodness of fit test and indicated a normal distribution for the response variable. The data were not transformed, but all numerical predictive variables were scaled (i.e., z-scores with the *scale* function in R). Statistical analyses were carried out using a 95% confidence interval ($\alpha = 0.05$), and model assumptions were validated with residual plots. Regression models were constructed in R v. 3.6.1.

Coral morpho-functional groups and community shifts

The functional diversity of coral communities was estimated using six different traits: skeletal density, growth rate, rugosity index, colony size, reproduction strategy, and corallite width (Tables S5, S6). Some or all these traits have been previously used in other studies to represent the functioning of reef-building corals in a multidimensional space^{34,71}. The information on species-level traits was obtained from different sources that provide comprehensive details for each selected trait (^{33,72,73}; Table S1). To better compare traits considering the contribution disparities between species (see ^{74,75}), the traits were categorized into numerical groups (1–5). Hierarchical clustering was performed to identify groups in the data set and estimate trait similarity. We then grouped the reef corals into morpho-functional groups using a Gower dissimilarity matrix ('vegan' package in R; ⁷⁶) and average-linkage hierarchical clustering, which calculates the average distance between clusters before merging ('cluster' package in R; ⁷⁷). Groups were defined using 65% dissimilarity because it was the most evident grouping and provided a concise number of groups (Fig. 1).

We measured the contribution of each species to compositional similarity within periods and dissimilarity between periods with a Similarity Percentage analysis (SIMPER; ⁷⁸). SIMPER identifies the species that are most responsible for the observed patterns (e.g., the species that typify each factor level and those that contribute the most to dissimilarity between levels) by disaggregating the Bray-Curtis similarities between samples. The more abundant a species is within a group, the more it contributes to intra-group similarity; species with consistently high contributions to the dissimilarity between groups are good discriminating species⁷⁹.

To explore temporal changes in coral composition and the traits of those assemblages, a principal component analysis (PCA) was performed using the 35 reef sites with pre- and post-outbreak information. We evaluated changes in coral-assemblage composition at species and family levels. Changes in functional trait assemblages were assessed through a Community-Weighted Means (CWM) analysis that calculates the relative contribution of a given trait to the coral assemblage, which largely determines ecosystem processes^{80,81}. Changes in the functional diversity of coral assemblages were evaluated with functional richness, which represent the volume of the convex hull covering all species in the functional space, and functional evenness, which measures the regularity of the abundance distribution in the functional space^{82,83}. These indices have been widely used to account for functional

diversity changes in coral communities^{84,85}. Statistical differences between periods were tested with a paired Welch's t-test. All statistical and functional diversity analyses were performed in R⁷⁰ using the 'FD' package⁸⁶.

Coral community calcification

To estimate the effects of SCTLD on the physical functionality of coral reefs, we calculated the potential calcification (i.e., kg CaCO₃ m⁻² yr⁻¹) of the coral assemblages for each period using the sum of the calcification rate of each colony proportional to the sampled reef area (m²). We used a reef-level estimation to calculate mean coral community calcification for each period. For this, we estimated the calcification rate of each colony within each study site considering the size, mean annual growth rate (cm yr⁻¹), mean skeletal density (g cm⁻³), and morphological growth of each species following the methodology described by Gonzalez-Barrios et al.⁸⁷ (see also ³²). For each period, the calcification rate was estimated as the annual volume of calcium carbonate accumulated by the living tissue of the colony for each time period using the information from the 35 resampled sites.

References

1. Weil, E. Coral Reef Diseases in the Wider Caribbean. in *Coral Health and Disease* (eds. Rosenberg, E. & Loya, Y.) 35–68 (Springer, 2004). doi:10.1007/978-3-662-06414-6_2
2. Harvell, C. D. *et al.* Coral diseases, Environmental drivers and the balance between corals and microbial associates. *Oceanography* **20**, 172–195 (2007).
3. Green, E. P. & Bruckner, A. W. The significance of coral disease epizootiology for coral reef conservation. *Biological Conservation* **96**, 347–361 (2000).
4. Alvarez-Filip, L., Estrada-Saldívar, N., Pérez-Cervantes, E., Molina-Hernández, A. & González-Barrios, F. J. A rapid spread of the Stony Coral Tissue Loss Disease outbreak in the Mexican Caribbean. *PeerJ* (2019). doi:10.7717/peerj.8069
5. Dungan, M. L., Miller, T. E. & Thomson, D. A. Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. *Science* **216**, 989–991 (1982).
6. Pounds, J. A. *et al.* Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167 (2006).
7. Nicholls, H. Mysterious die-off sparks race to save saiga antelope. *Nature* 1–2 (2015). doi:10.1038/nature.2015.17675
8. Daszak, P., Cunningham, A. A. & Hyatt, A. D. Emerging infectious diseases of wildlife - Threats to biodiversity and human health. *Science* **287**, 443–449 (2000).
9. Peters, E. C. Diseases of Coral Reef Organisms. in *Coral Reefs in the Anthropocene* (ed. Birkeland, C.) 147–178 (Springer Netherlands, 2015). doi:10.1007/978-94-017-7249-5_8
10. Lessios, H. A., Robertson, D. R. & Cubitt, J. D. Spread of *Diadema* mass mortality through the Caribbean. *Science* **226**, 335–337 (1984).
11. Perry, C. T. & Alvarez-Filip, L. Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology* **33**, 976–988. (2019).
12. Aronson, R. B. & Precht, W. F. White-band disease and the changing face of Caribbean coral reefs. in *Hydrobiologia* **460**, 25–38 (2001).
13. Alvarez-Filip, L., Dulvy, N. K., Gill, J. a, Côté, I. M. & Watkinson, A. R. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings. Biological sciences / The Royal Society* **276**, 3019–25 (2009).
14. Estrada-Saldívar, N., Jordán-Dahlgren, E., Rodríguez-Martínez, R. E., Perry, C. T. & Alvarez-Filip, L. Functional consequences of the long-term decline of reef-building corals in the Caribbean: evidence of across-reef functional convergence. *Royal Society Open Science* **6**, 1–15 (2019).
15. Cramer, K. L. *et al.* Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. *Science Advances* **6**, (2020).
16. Bruno, J. F. *et al.* Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology* **5**, 1220–1227 (2007).
17. Vega Thurber, R. *et al.* Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. *Global Change Biology* **20**, 544–554 (2014).

18. Wear, S. L. & Thurber, R. V. Sewage pollution: Mitigation is key for coral reef stewardship. *Annals of the New York Academy of Sciences* **1355**, 15–30 (2015).
19. Randall, C. J. & Van Woesik, R. Some coral diseases track climate oscillations in the Caribbean. *Scientific Reports* **7**, 1–8 (2017).
20. Lapointe, B. E., Brewton, R. A., Herren, L. W., Porter, J. W. & Hu, C. *Nitrogen enrichment , altered stoichiometry , and coral reef decline at Looe Key , Florida Keys , USA : a 3 - decade study*. *Marine Biology* **166**, (Springer Berlin Heidelberg, 2019).
21. Precht, W. F., Gintert, B. E., Robbart, M. L., Fura, R. & van Woesik, R. Unprecedented Disease-Related Coral Mortality in Southeastern Florida. *Scientific Reports* **6**, 1–11 (2016).
22. Kramer, P. R., Roth, L. & Lang, J. Map of Coral Cover of Susceptible Coral Species to SCTLD. (2020). Available at: www.agrra.org. ArcGIS Online.
23. Aeby, G. S. *et al.* Pathogenesis of a Tissue Loss Disease Affecting Multiple Species of Corals Along the Florida Reef Tract. *Frontiers in Marine Science* **6**, 1–18 (2019).
24. Iwanowicz, D. D. *et al.* Exploring the Stony Coral Tissue Loss Disease Bacterial Pathobiome. *Journal of Chemical Information and Modeling* **53**, 1689–1699 (2019).
25. Meyer, J. L. *et al.* Microbial community shifts associated with the ongoing stony coral tissue loss disease outbreak on the Florida Reef Tract. *Frontiers in Microbiology* 626408 (2019). doi:10.1101/626408
26. Gintert, B. E. *et al.* Regional coral disease outbreak overwhelms impacts from local dredge project. *Environmental Monitoring and Assessment* **191**, 1–39 (2019).
27. Muller, E. M., Sartor, C., Alcaraz, N. I. & van Woesik, R. Spatial Epidemiology of the Stony-Coral-Tissue-Loss Disease in Florida. *Frontiers in Marine Science* **7**, 11 (2020).
28. Estrada-Saldívar, N., Quiroga-García, B. A., Pérez-Cervantes, E., Rivera-Garibay, O. O. & Alvarez-Filip, L. Effects of the Stony Coral Tissue Loss Disease Outbreak on Coral Communities and the Benthic Composition of Cozumel Reefs. *Frontiers in Marine Science* **8**, 1–13 (2021).
29. Neely, K. L., Lewis, C. L., Lunz, K. & Kabay, L. Rapid population decline of the Pillar coral *Dendrogyra cylindrus* along the Florida Reef Tract. *Frontiers in Marine Science* **8**, (2021).
30. Rippe, J. P., Kriefall, N. G., Davies, S. W. & Castillo, K. D. Differential disease incidence and mortality of inner and outer reef corals of the upper Florida Keys in association with a white syndrome outbreak. *Bulletin of Marine Science* **95**, 305–316 (2019).
31. Sharp, W. C., Shea, C. P., Maxwell, K. E., Muller, E. M. & Hunt, J. H. Evaluating the small-scale epidemiology of the stony-coral -tissue-loss-disease in the middle. *PLOS ONE* **15**, 1–25 (2020).
32. Estrada-Saldívar, N. *et al.* Reef-scale impacts of the stony coral tissue loss disease outbreak. *Coral Reefs* (2020). doi:10.1007/s00338-020-01949-z
33. González-Barrios, F. J., Cabral-Tena, R. A. & Alvarez-Filip, L. Recovery disparity between coral cover and the physical functionality of reefs with impaired coral assemblages. *Global Change Biology* **27**, 640–651 (2021).
34. McWilliam, M. *et al.* Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences* **115**, 3084–3089 (2018).
35. Perry, C. T. *et al.* Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Global Change Biology* **21**, 1153–1164 (2015).
36. Toth, L. T. *et al.* The unprecedented loss of Florida's reef-building corals and the emergence of a novel coral-reef assemblage. *Ecology* e02781 (2019). doi:10.1002/ecy.2781
37. Alves, C. *et al.* Twenty years of change in benthic communities across the Belizean Barrier Reef. *bioRxiv Preprint*, 1–36 (2021).
38. Bruno, J. F. Implications for Reef Restoration Efforts. *Science* **345**, 879–880 (2014).
39. Rodríguez-Martínez, R. E., Banaszak, A. T., McField, M. D., Beltrán-Torres, A. & Alvarez-Filip, L. Assessment of *Acropora palmata* in the mesoamerican reef system. *PLoS ONE* **9**, 1–7 (2014).
40. Mudge, L., Alves, C., Figueroa-Zavala, B. & Bruno, J. Assessment of Elkhorn Coral Populations and Associated Herbivores in Akumal, Mexico. *Frontiers in Marine Science* **6**, 1–12 (2019).
41. Baums, I. B., Miller, M. W. & Hellberg, M. E. Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology* **14**, 1377–1390 (2005).
42. Patterson, K. L. *et al.* The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata*. *Proceedings of the National Academy of Sciences* **99**, 8725–8730 (2002).

43. Edmunds, P. J. & Elahi, R. The demographics of a 15-year decline in covers of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs* **77**, 3–18 (2007).
44. Eakin, C. M. *et al.* Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* **5**, (2010).
45. Suchley, A. & Alvarez-Filip, L. Local human activities limit marine protection efficacy on Caribbean coral reefs. *Conservation Letters* **11**, 1–9 (2018).
46. Perry, C. T. *et al.* Loss of coral reef growth capacity to track future increases in sea-level. *Nature* **558**, 396–400 (2018).
47. Enochs, I. C. *et al.* Ocean acidification enhances the bioerosion of a common coral reef sponge: Implications for the persistence of the Florida Reef Tract. *Bulletin of Marine Science* **91**, 271–290 (2015).
48. Perry, C. T. *et al.* Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20142018–20142018 (2014).
49. Molina-Hernández, A., González-Barrios, F. J., Perry, C. T. & Álvarez-Filip, L. Two decades of carbonate budget change on shifted coral reef assemblages: Are these reefs being locked into low net budget states?: Caribbean reefs carbonate budget trends. *Proceedings of the Royal Society B: Biological Sciences* **287**, (2020).
50. Andersson, A. J. & Gledhill, D. Ocean acidification and coral reefs: Effects on breakdown, dissolution, and net ecosystem calcification. *Annual Review of Marine Science* **5**, 321–348 (2013).
51. Tribollet, A., Chauvin, A. & Cuet, P. Carbonate dissolution by reef microbial borers: a biogeological process producing alkalinity under different pCO₂ conditions. *Facies* **65**, 1–10 (2019).
52. Costa, S. V. *et al.* Diversity and Disease: The Effects of Coral Diversity on Prevalence and Impacts of Stony Coral Tissue Loss Disease in Saint Thomas, U.S. Virgin Islands. *Frontiers in Marine Science* **8**, (2021).
53. Veron, J., Stafford-Smith, M., DeVantier, L. & Turak, E. Overview of distribution patterns of zooxanthellate Scleractinia. *Frontiers in Marine Science* **2**, 1–19 (2015).
54. Miller, M. W., Lohr, K. E., Cameron, C. M., Williams, D. E. & Peters, E. C. Disease dynamics and potential mitigation among restored and wild staghorn coral, *Acropora cervicornis*. *PeerJ* **2014**, 1–30 (2014).
55. Hughes, A. R. & Stachowicz, J. J. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 8998–9002 (2004).
56. Sokolow, S. H., Foley, P., Foley, J. E., Hastings, A. & Richardson, L. L. Disease dynamics in marine metapopulations: Modelling infectious diseases on coral reefs. *Journal of Applied Ecology* **46**, 621–631 (2009).
57. Bellwood, D. R. *et al.* Coral reef conservation in the Anthropocene: Confronting spatial mismatches and prioritizing functions. *Biological Conservation* **236**, 604–615 (2019).
58. Grosso-Becerra, M. V., Mendoza-Quiroz, S., Maldonado, E. & Banaszak, A. T. Cryopreservation of sperm from the brain coral *Diploria labyrinthiformis* as a strategy to face the loss of corals in the Caribbean. *Coral Reefs* **40**, 937–950 (2021).
59. Edmunds, P. J. Long-term dynamics of coral reefs in St. John, US Virgin Islands. *Coral Reefs* **21**, 357–367 (2002).
60. Vermeij, M. J. A. Early life-history dynamics of Caribbean coral species on artificial substratum: The importance of competition, growth and variation in life-history strategy. *Coral Reefs* **25**, 59–71 (2006).
61. Webster, F. J., Babcock, R. C., Van Keulen, M. & Loneragan, N. R. Macroalgae inhibits larval settlement and increases recruit mortality at Ningaloo Reef, Western Australia. *PLoS ONE* **10**, 1–14 (2015).
62. Suchley, A., McField, M. D. & Alvarez-Filip, L. Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs. *PeerJ* **4**, e2084 (2016).
63. Contreras-Silva, A. *et al.* A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican caribbean. 1–12 (2020). doi:10.1038/s41598-020-65801-8
64. Meiling, S. S., Muller, E. M., Smith, T. B. & Brandt, M. E. 3D Photogrammetry Reveals Dynamics of Stony Coral Tissue Loss Disease (SCTLD) Lesion Progression Across a Thermal Stress Event. *Frontiers in Marine Science* **7**, 1–12 (2020).
65. Lang, J. C., Marks, K. W., Kramer, P. R. & Kramer, P. A. Protocolos AGRRA 5.5. 1–44 (2012).

66. Burke, L., Reyttar, K., Spalding, M. & Perry, A. *Reefs at risk*. *National Geographic* (2011). doi:10.1016/0022-0981(79)90136-9
67. Espinosa-Andrade, N., Suchley, A., Reyes-Bonilla, H. & Alvarez-Filip, L. The no-take zone network of the Mexican Caribbean: assessing design and management for the protection of coral reef fish communities. *Biodiversity and Conservation* **0123456789**, (2020).
68. Chollett, I., Müller-Karger, F. E., Heron, S. F., Skirving, W. & Mumby, P. J. Seasonal and spatial heterogeneity of recent sea surface temperature trends in the Caribbean Sea and southeast Gulf of Mexico. *Marine Pollution Bulletin* **64**, 956–965 (2012).
69. Cox, C., Valdivia, A., McField, M., Castillo, K. & Bruno, J. F. Establishment of marine protected areas alone does not restore coral reef communities in Belize. *Marine Ecology Progress Series* **563**, 65–79 (2017).
70. Core Team, R. R: A language and environment for statistical computing. R Foundation for Statistical Computing. *Vienna, Austria*: URL <https://www.R-project.org/> (2020).
71. Hughes, T. P. *et al.* Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83 (2018).
72. Riddle, D. Coral reproduction, part one: A natural coral spawning in Hawaii, The cauliflower coral (*Pocillopora meandrina*). *Advanced Aquarist's Online Magazine* **7**, 10–16 (2008).
73. Madin, J. S. *et al.* The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data* **3**, 160017 (2016).
74. Hughes, T. P. *et al.* Global warming transforms coral reef assemblages. *Nature* (2018). doi:10.1038/s41586-018-0041-2
75. McWilliam, M., Pratchett, M. S., Hoogenboom, M. O. & Hughes, T. P. Deficits in functional trait diversity following recovery on coral reefs. *Proceedings of the Royal Society B: Biological Sciences* **287**, (2020).
76. Oksanen, J. Vegan: community ecology package version 1.8-6. <http://cran.r-project.org> (2007).
77. Maechler, M. *et al.* Package 'cluster'. *Dosegljivo na* (2013).
78. CLARKE, K. R. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143 (1993).
79. Clarke, K. R. & Warwick, R. M. Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition. Primer-E, Plymouth. *Plymouth, United Kingdom: PRIMER-E* 172 (2001).
80. Lavorel, S. *et al.* Assessing functional diversity in the field - Methodology matters! *Functional Ecology* **22**, 134–147 (2008).
81. Ricotta, C. & Moretti, M. CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia* **167**, 181–188 (2011).
82. Villéger, S., Mason, N. W. H. & Mouillot, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301 (2008).
83. Mouillot, D. *et al.* Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS Biology* **11**, (2013).
84. Denis, V., Ribas-Deulofeu, L., Sturaro, N., Kuo, C. Y. & Chen, C. A. A functional approach to the structural complexity of coral assemblages based on colony morphological features. *Scientific Reports* **7**, 1–11 (2017).
85. Teixidó, N. *et al.* Functional biodiversity loss along natural CO2 gradients. *Nature Communications* **9**, 1–9 (2018).
86. Laliberté, E., Legendre, P., Shipley, B. & Laliberté, M. E. Package 'FD'. *Measuring functional diversity from multiple traits, and other tools for functional ecology* (2014).
87. González-Barrios, F. J. & Alvarez-Filip, L. A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. *Ecological Indicators* **95**, 877–886 (2018).

Acknowledgments: This study was supported by the Mexican Council of Science and Technology (CONACyT, grant number: FORDECYT-PRONACES/425888/2020), the Comisión Nacional de Áreas Naturales Protegidas of Mexico (grant number: PROREST/CER/56/2019), the Universidad Nacional Autónoma de México (UNAM; UNAM-DGAPA-PAPIIT grant number: IN-205019), and a Royal Society Newton Advanced Fellowship (grant number: NA150360).

Author contributions: Conceptualization, Funding acquisition, Project administration, and Writing original draft: LA-F; Methodology and Investigation: LA-F, FJG-B, EP-C, AM-H, NE-S; Data curation:

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652 **Competing interests:** Authors declare that they have no competing interests.

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654 **Data and materials availability:** All data are available in the main text or the supplementary materials.

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