

RESEARCH ARTICLE

Recurrent Crown-of-Thorns Starfish (*Acanthaster cf. solaris*) Outbreaks Alter Coral Recovery Trajectories in the Central South China Sea

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Tracking the degradation and recovery of foundational organisms is key to understanding ecosystem sustainability. Using coral reefs as a model, we investigated how disturbance frequency affects the recovery of reef-building corals. We examined changes in coral cover, α - and β -taxonomic diversity, functional diversity, and community structure over 3 periods (2006, 2013–2015, and 2022) across 14 sites on 2 atolls in the central South China Sea, where crown-of-thorns starfish outbreaks occurred at different frequencies. Building on 2006 baseline surveys prior to crown-of-thorns starfish-induced decline, our 2013–2015 assessments captured early postoutbreak structural recovery alongside localized degradation associated with thermal stress. Recurrent outbreaks at Yongle Atoll were associated with further community degradation, with communities shifting toward dominance by structurally simpler species. Despite a decline in the overall species and functional composition of communities, β -diversity decomposition revealed that coral communities retained a trend toward functional diversification after repeated outbreaks, meaning that species and functional compositions at individual sites are likely more simplified than anticipated. At Xuande Atoll, which experienced only one major outbreak, coral cover, species richness, and functional diversity at some sites recovered to predisturbance levels within 16 years, despite intermittent thermal stress inhibiting the rate of recovery. However, community structure recovery lags behind, as the delayed recovery of structurally complex groups (e.g., corymbose and table corals) constrains the overall community recovery. Overall, while coral communities can demonstrate recovery potential, repeated disturbances disrupt this process. Therefore, effective conservation must focus on protecting sensitive functional groups and mitigating the frequency of disturbances.

Introduction

Global changes have substantially impacted both terrestrial and marine ecosystems, including forests and coral reefs, leading to varying degrees of degradation of these ecosystems [1,2]. The degradation ecosystems can undergo secondary succession and gradually recover after disturbances [3]. However, ongoing disturbance events prevent most degraded communities from completely returning to their previous state [4,5]. The future fate of degraded communities depends on their resistance to disturbances and their ability to recover [3,6]. Therefore, it is crucial to track the degradation process of communities following disturbances and their ability to recover to predisturbance species compositions under recurrent disturbances [7,8].

Coral reef ecosystems serve as case ecosystems for studying the effects of recurrent disturbance on community degradation and recovery. Nearly all coral reefs worldwide have degraded to intermediate states [7]. Disturbance to coral reef ecosystems can be caused by abnormal sea temperatures, typhoons, extreme rainfall, and acidification, resulting from global climate change, as well as by human activity and by outbreaks of corallivorous organisms [2,7,9,10]. Model projections indicated that the frequency of extreme ocean climate events, such as marine heatwaves and typhoons, is expected to increase in the future [5,8]. This will likely increase the frequency of mass coral bleaching events and further degrade coral reefs [7,11]. Meanwhile, the outbreak of corallivorous organisms such as crown-of-thorns starfish (CoTS) has also occurred frequently on coral reefs [12].

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While present at background densities (e.g., less than 15 CoTS per hectare) on healthy reefs [13], high-density CoTS outbreaks can rapidly consume large amounts of coral, leading to coral death and causing short-term or long-term declines in coral cover, potentially reducing it to critical levels (below 0.1%) [14,15]. These compounded disturbances exacerbate the stress on coral ecosystems, making it more challenging for them to recover from degradation.

Analyzing the effect of disturbances on foundational species is particularly urgent because these dominant habitat-forming organisms are often disproportionately affected by disturbances [16,17]. Reef-building corals, which create complex 3-dimensional structures through their skeletons, are foundational species in coral reef ecosystems [18]. A key indicator of coral reef degradation is the decline in coral coverage of reef-building corals, which has halved since the 1950s [2]. Besides biomass loss, the structure of coral assemblages has consistently changed during degradation [19,20]. Studies have shown that persistent disturbances have led to a global shift in coral community structure: Complex species (such as branching corals) are declining in favor of simpler forms (massive, submassive, and encrusting) in recent decades, resulting in the homogenization of both the species composition and functional structure of degraded coral communities [19,21].

Degraded coral communities can enter successional recovery phases and return to predegradation community states within 2 to 10 years [3,22,23]. However, severe or recurrent disturbances can arrest this recovery, causing communities to persist at low coral cover and hindering a return to their original state [24]. A critical knowledge gap lies in understanding how disturbance frequency, in particular, shapes these recovery trajectories [17]. In this study, we capitalize on a unique opportunity in 2 atolls located in the Xisha Islands in the central South China Sea. These atolls experienced a severe outbreak of CoTS (*Acanthaster cf. solaris*) between 2006 and 2010 and again between 2019 and 2022 [25–27]. Frequent disturbances accompanied by thermal stress also occurred during these periods [26,28,29]. To understand the dynamics of coral communities in the Xisha Islands under different frequencies of disturbance, this study selected 2 atolls:

Yongle Atoll, which experienced recurrent CoTS outbreaks, and Xuande Atoll, which experienced a single CoTS outbreak. The objective was to reveal whether and how recurrent CoTS outbreak disturbances alter recovery capacity, biodiversity patterns, and community assembly processes of reef-building corals. We hypothesize that Yongle Atoll, subjected to recurrent CoTS disturbances, will exhibit low coral cover alongside low α - and β -taxonomic and functional diversity. In contrast, Xuande Atoll, which did not experience the second CoTS outbreak, is expected to recover to coral cover and community structure similar to preoutbreak conditions, even in the presence of thermal stress disturbance. This comparison aims to elucidate the impact of recurrent disturbances on coral reef resilience and the potential for recovery in different disturbance scenarios.

Materials and Methods

Study area and study design

The Xisha Islands are located in the central South China Sea (Fig. 1A), and this study focuses on the Xuande Atoll (Fig. 1B) and Yongle Atoll (Fig. 1C) within the Xisha Islands. To clarify the frequency of disturbances affecting the 2 atolls in the Xisha Islands, we collected data on key factors including sea surface temperature anomalies and the timing of CoTS outbreaks influencing coral communities in the region. Degree Heating Week (DHW) data were assessed using daily 5-km regional virtual station data provided by National Oceanic and Atmospheric Administration Coral Reef Watch (<https://coralreefwatch.noaa.gov>). Data on CoTS outbreaks in the Xisha Islands from 2006 to 2018 were obtained from Li et al. [26]. In addition, records of CoTS outbreaks in the 2 atolls were collected from the CNKI and Web of Science databases using the keywords “Xisha” (or “Paracel”) and “Crown-of-Thorns Starfish” (or “*Acanthaster*”) (Table S1).

Across the entire Xisha Islands, the average density reached 1,860 individuals per hectare in 2006 and further increased to 2550 individuals per hectare by 2009 [28]. More recently, localized surveys at Yongle Atoll recorded densities exceeding 1,000 individuals per hectare in 2019 [26], with levels still above 500 individuals per hectare in 2021 [25]. All these recorded densities

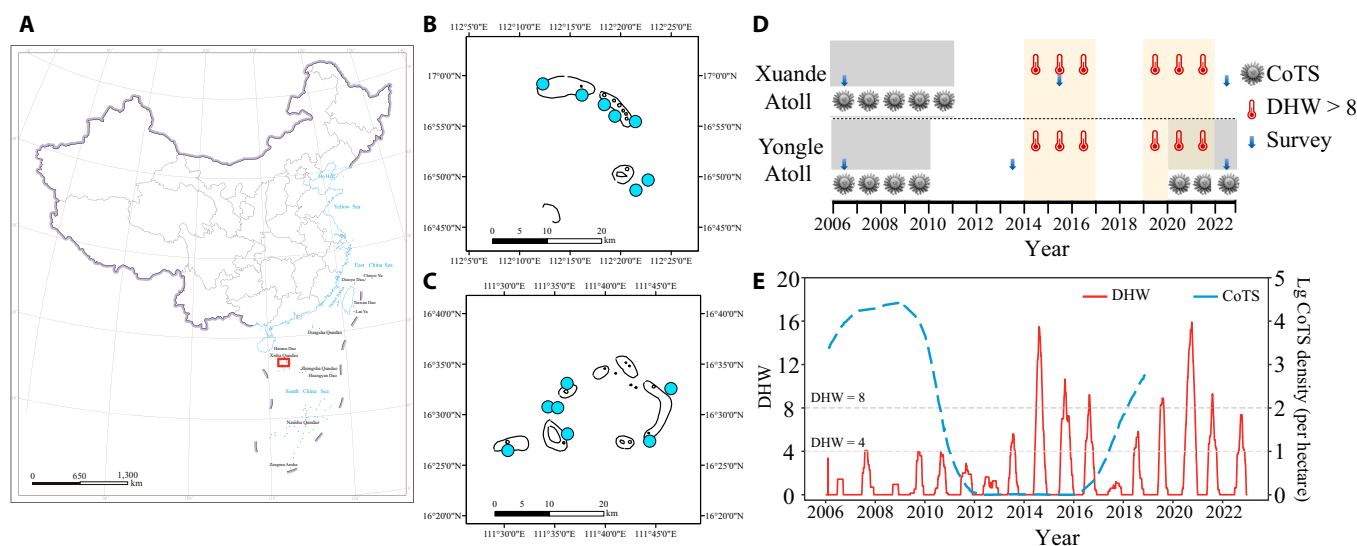


Fig. 1. Map of coral community survey areas and their disturbance in the Xisha Islands. (A) Coral community survey area in the South China Sea. (B) Survey sites in Xuande Atoll. (C) Survey sites in Yongle Atoll. (D) Disturbance event records of Xuande Atoll and Yongle Atoll from 2006 to 2022. (E) Map of the Degree Heating Week (DHW) (2006–2022) and density of crown-of-thorns starfish (CoTS) (2006–2018) in the Xisha Islands. Lg, the base-10 logarithm function.

are substantially higher than the established outbreak threshold of 15 individuals per hectare [13], confirming that the region has been experiencing sustained CoTS outbreaks. Therefore, the outbreak of CoTS in the Xisha Islands can be divided into 3 stages (Fig. 1B and C): Full-scale outbreak (2006–2010): CoTS outbreaks occurred on nearly all reefs in the Xisha Islands [28]; no outbreak (2011–2019): CoTS outbreaks subsided, and no significant outbreaks were recorded [26]; regional outbreak (2019 to present): Since 2019, CoTS outbreaks have reemerged in Yongle Atoll, while no outbreaks have been observed in Xuande Atoll [25,30]. This study established 7 survey sites in each atoll (Fig. 1B and C) and conducted coral community assessments during 3 key periods: the baseline at the onset of the outbreak (2006), after the outbreak subsided (2013–2015), and during the localized second outbreak (2022). It should be noted that, although the density of the CoTS had already exceeded the outbreak threshold in 2006, coral cover and diversity metrics at that time still represented a near-intact state preceding the bulk of the coral loss that unfolded in the following years [26,28].

Field survey and species identification

To assess changes in coral species communities, this study conducted surveys using the point-intercept transect method across 14 reef sites. SCUBA (self-contained underwater breathing apparatus) diving was used to establish 3 survey transects at depths ranging from 3 to 15 m. The coral community along each transect was recorded using an underwater camera. A point-intercept approach at 10-cm intervals was applied to identify the coral species directly beneath the transect line from the video footage. In 2006, each survey site used a 50-m transect, whereas in subsequent survey years, 6 replicate 10-m transects were used per depth at each site. Reef-building corals were identified to species level, although species within *Acropora*, *Montipora*, *Goniopora*, and *Porites* were classified only to genus level with growth forms due to identification challenges. The growth forms of corals were identified on the basis of Corals of the World (<https://www.coralsoftheworld.org>), and we combined them with coral cover to confirm the coverage change of coral with different growth forms (Fig. S1). In selected cases, coral fragments were collected for laboratory analysis and precise species identification. To maintain consistency in species identification across survey years, all records were standardized according to the updated taxonomy of Scleractinia provided by the World Register of Marine Species (<http://marinespecies.org>). To prevent ambiguity with “soft coral”, the term “coral” hereafter specifically denotes “reef-building coral”.

Statistical analyses

Biodiversity indices

The diversity of corals was quantified across multilevel. For taxonomic diversity, the richness of reef-building coral species was calculated as the number of species recorded in the transect. Due to differences in survey area across years, we assessed whether species richness was adequately surveyed by calculating sample coverage using the iNext function [31].

For functional diversity, corals are foundational species in coral reefs because they are the primary architects of reef structures; thus, we centered our analysis on coral functional roles, especially habitat-forming traits. Following McWilliam et al. [32], we built trait space using 7 coral traits: growth rate, skeletal density, coral-lite width, colony size, height, surface-area-to-volume ratio, and intracolony space size. Species-level trait data were sourced from the Coral Traits Database [33]. Unmeasured traits were populated

via the approach of Madin et al. [34]: a regression model using coral growth form and phylogenetic relationships to infer missing values (including genus-level data). All traits were then scaled to numerical categories (1 to 5) as in McWilliam et al. [32]. Subsequently, principal coordinate analysis based on the Gower distance matrix was used to analyze 7 functional traits and construct the functional space of different coral communities. Functional diversity was measured as the trait space volume occupied by each community across 4 dimensions.

To investigate the degree of variation in species composition and functional trait composition within coral communities during the same survey year, we used a decomposition approach for β -diversity. β -Taxonomic and -functional diversity were calculated as pairwise dissimilarity matrices using the betapart package in R, which partitions total dissimilarity into turnover and nestedness components. We applied the Bray–Curtis index for taxonomic data and the Sørensen index for functional data. To assess disparities in biodiversity indices of communities between the 2 atolls across 3 survey years, we used the Kruskal–Wallis nonparametric test due to the nonuniform variance in the data. Subsequently, for multiple comparisons, we utilized Dunn’s test of nonparametric test.

Community structure analysis

To analyze differences in community structure over time and between atolls, distance-based redundancy analysis (db-RDA) was performed using the Bray–Curtis distance metric to identify dominant taxa contributing to community differences. A step-wise regression approach was applied to optimize the selection of key genera, with variables added sequentially on the basis of their ability to explain coral community structure variation according to the Akaike information criterion. The final db-RDA analysis incorporated the combination of genera that resulted in the lowest Akaike information criterion value. In addition, permutational multivariate analysis of variance (PERMANOVA) with 999 permutations were used to assess differences in coral community structure across survey periods.

Functional trait trajectories

In addition, to understand how the overall functional traits of coral communities in the 2 Xisha Islands changed over time, principal components analysis (PCA) was performed using community-weighted means of traits. The PCA data matrix was composed of the community-weighted means values for each surveyed coral community across different years. PCA ensured comparability of all traits on the same scale. Finally, a 2-dimensional PCA plot was generated, illustrating the functional composition trajectories of each surveyed coral community over time.

Results

Disturbance history in the Xisha Islands

The analysis of disturbance factors in the Xisha Islands indicates that the region experienced multiple disturbances between 2006 and 2022, including CoTS outbreaks and abnormal sea temperature increases. The DHW curve shows that $DHW > 8$ in the periods 2014–2016 and 2019–2021, suggesting that coral communities across the Xisha Islands were subjected to heat stress (Fig. 1D and E and Table S1). In addition, recorded coral bleaching events from 2014 to 2019 further support the findings from remote sensing data. Records of CoTS outbreaks indicate that, after 2020, CoTS outbreaks reoccurred at Yongle Atoll, whereas no outbreaks have been detected at Xuande Atoll s (Fig. 1D and E and Table S1).

Coral cover, species richness and assemblages' composition

The results of coral cover indicated a continuous decline at Yongle Atoll, with coverage decreasing from 52.32% in 2006 to 25.64% in 2013 and further to 18.36% in 2022 (Fig. 2A and B).

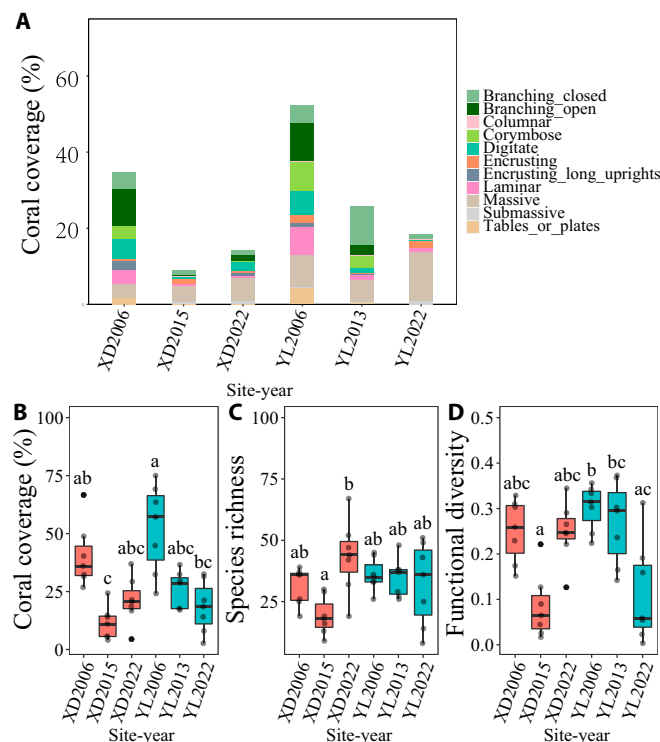


Fig. 2. Coral cover variation and biodiversity parameters variation in the Xisha Islands from 2006 to 2022. (A) The composition of coral with different growth forms across various years; (B) coral cover variation; (C) species richness variation; (D) functional diversity variation. Letters are labeled as Dunn test results. Examples of underwater photographs depicting different growth forms of coral can be found in Fig. S1.

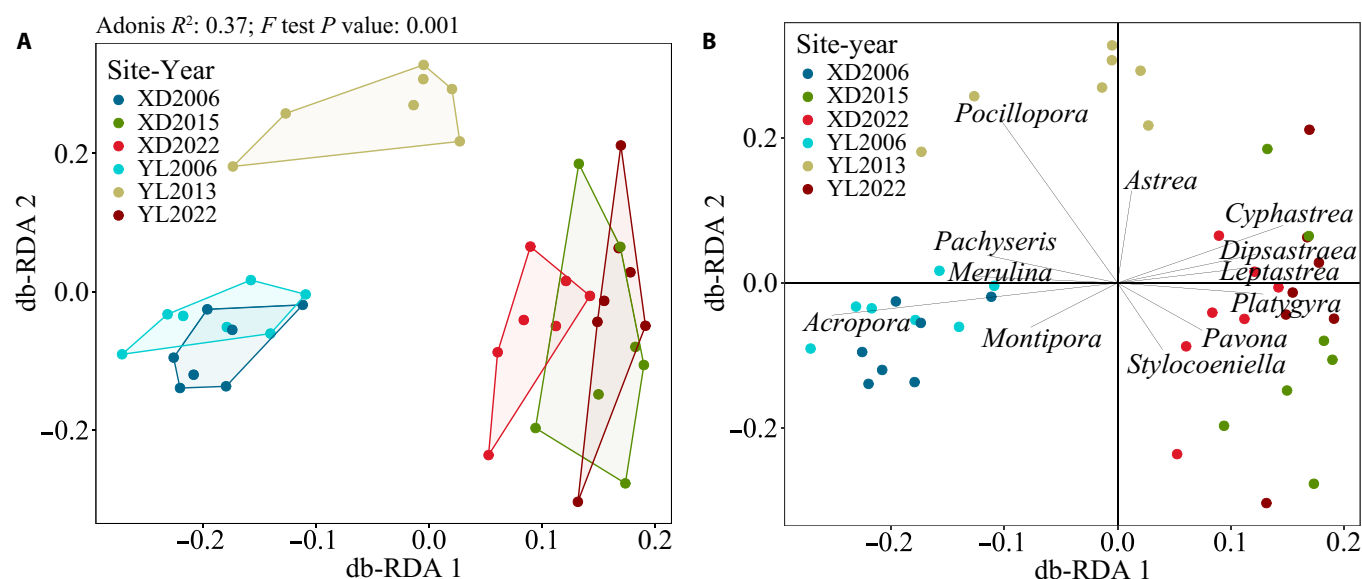


Fig. 3. Coral community structure in Xisha Islands. (A) Permutational multivariate analysis of variance (PERMANOVA) results shown by distance-based redundancy analysis (db-RDA). (B) db-RDA showing the distribution of different coral genus-level taxonomic orders in the community, with the top 12 most influential coral genera shown in the figure.

In contrast, Xuande Atoll exhibited a decline, followed by a partial recovery, with coral cover dropping from 40.36% in 2006 to 11.35% in 2015 and then rising to 21.15% in 2022. However, the coral cover in 2022 had not yet returned to the 2006 levels (Fig. 2A and B).

The rarefaction analysis indicated that despite slight differences in sampling area each year, the sample coverage for each coral community exceeded 97%, suggesting that the surveys adequately captured the coral species diversity across all years (Fig. S2). No significant changes were observed in species diversity at Xuande Atoll and Yongle Atoll (Fig. 2C). However, the coral community structure changed significantly and could be clearly distinguished by year.

In 2006, the coral communities of Yongle Atoll and Xuande Atoll were similar, characterized by branching corals, with species from the *Acropora* genus being dominant (Fig. 3A and B). The main growth forms included branching closed, branching open, digitate, and corymbose corals (Fig. 2A). At Yongle Atoll, branching corals had a 34.09% coverage, accounting for 65.16% of the total coral cover, while at Xuande Atoll, branching corals had a 26.95% coverage, representing 66.77% of the total coral cover (Fig. 2A). By 2022, Yongle Atoll and by 2015, Xuande Atoll exhibited degraded coral communities, dominated by species from the *Cyphastrea*, *Dipsastraea*, *Platygyra*, and *Leptastrea*, primarily in massive growth forms (Fig. 3A and B). In 2022, the massive coral cover at Yongle Atoll was 12.79%, making up 69.66% of the total coral cover, while in 2015, branching corals at Xuande Atoll had declined to 3.95%, accounting for only 34.80% of the total coral cover (Fig. 2A).

In 2013, Yongle Atoll was in a transitional phase between degradation and its original state, characterized by the dominance of *Pocillopora* corals, with a coverage of 10.92%, representing 42.57% of the total coral cover (Fig. 3B). In 2022, Xuande Atoll also exhibited signs of recovery following degradation. Some coral communities showed a trend toward recover resembling the 2006 coral communities, but there were still significant differences compared to the original community structure (Fig. 3A).

Functional trait parameters

The 2 atolls showed different trends of functional changes during the monitoring period. For Xuande Atoll, functional diversity initially declined and then increased, and the functional diversity has returned to its initial state. In 2006, the functional diversity of Xuande Atoll was 0.2507, which decreased to 0.0844 in 2013 and then increased to 0.2486 in 2022 (Fig. 2D). However, there were no significant differences in functional diversity across the years of survey. In contrast, Yongle Atoll showed a continuous decline in functional diversity over the years. In 2006, the functional diversity of Yongle Atoll was 0.3024, which decreased to 0.2688 in 2013 and further dropped to 0.1146 in 2022, and the functional diversity in 2022 was significantly lower than in 2006 (Fig. 2D).

The results of the functional trait change trajectory indicated that the coral community of Yongle Atoll showed a consistent declining trend (Fig. 4B), with coral species moving toward lower growth rates, lower surface area to volume ratios, and reduced space gaps (Fig. 4C). The complex structure of the corals was continuously being lost and replaced by species with simpler structures but larger corallite width. In contrast, Xuande Atoll had degraded to a condition similar to Yongle Atoll's 2022 state by 2015, but after 7 years, its community's functional diversity began to recover toward the 2006 level (Fig. 4A). Further comparison of coral communities' assemblage reveals that the branching coral species of Xuande Atoll have returned to the community (Fig. S3). However, the recovery of corymbose branching corals and tabular branching corals has been delayed, which may be a key factor influencing the overall recovery of the coral community's functional trajectory (Fig. S3).

β -Diversity parameters

The β -diversity results indicated that the β -taxonomic diversity in the 2 atoll communities is contributed by the turnover component (Fig. 5A to C). The β -functional diversity, however, was jointly constituted by turnover and nestedness components of nearly equal magnitude (Fig. 5D to F). Compared to 2006, the overall and decomposed β -taxonomic diversity and β -functional diversity of Xuande Atoll remained unchanged in 2022 (Fig. 5A to F). However, both the overall β -taxonomic diversity and β -functional diversity of Yongle Atoll showed an increase, with

both increases jointly attributable to the rise in the turnover and nestedness components (Fig. 5A to F).

Discussion

Rapid degradation of coral communities under the outbreak of CoTS

High densities of pest species can lead to rapid declines in the biomass of target species. For example, in forest ecosystems, outbreaks of insect pests or pathogenic fungal infestations can lead to a swift decrease in tree cover [16]. In marine ecosystems, outbreaks of jellyfish such as *Aurelia* spp. and sea stars such as *Asterias amurensis* can diminish yields of commercial species [35]. Both types of outbreaks can potentially result in the rapid degradation of ecosystem structure and function [16,17]. Similarly, outbreaks of CoTS can cause a rapid decline in coral cover, even leading to coral depletion. In French Polynesia, high densities of CoTS led to systematic coral loss on Moorea Island, killing 96% of the corals in the area from 2005 to 2010 [14]. In the South China Sea, an outbreak of CoTS on Taiping Island reduced coral cover from 33% to less than 1% from 2017 to 2021 [15]. Our results from Yongle and Xuande strongly align with those from the results of long-term monitoring reports from the Xisha Islands, which show that the 2006 CoTS outbreak led to a decline in coral cover across the Xisha Islands, including Xuande Atoll and Yongle Atoll, from 60% in 2006 to less than 10% in 2011 [26,28,29], indicating that CoTS outbreaks in the early 21st century lead to rapid degradation of coral biomass in Xisha Islands.

Disturbances can lead to changes in community species composition and functional traits, but different types of disturbances have varying impacts on communities. In the case of pest outbreaks, their effect on community species depends on whether they exhibit feeding or infection preferences. Multiple studies have shown that CoTS exhibit selective feeding behavior, with a strong preference for consuming *Acropora* corals [10]. The results of this study also indicated that, following the CoTS outbreak in 2006, the community shifted from being dominated by *Acropora* to being dominated by other coral species and the 2014–2016 thermal stress event in the Xisha Islands may have further contributed to this transformation [20]. Such shifts in community structure have also been observed in other reefs affected by CoTS outbreaks [20,36–38]. Since *Acropora*

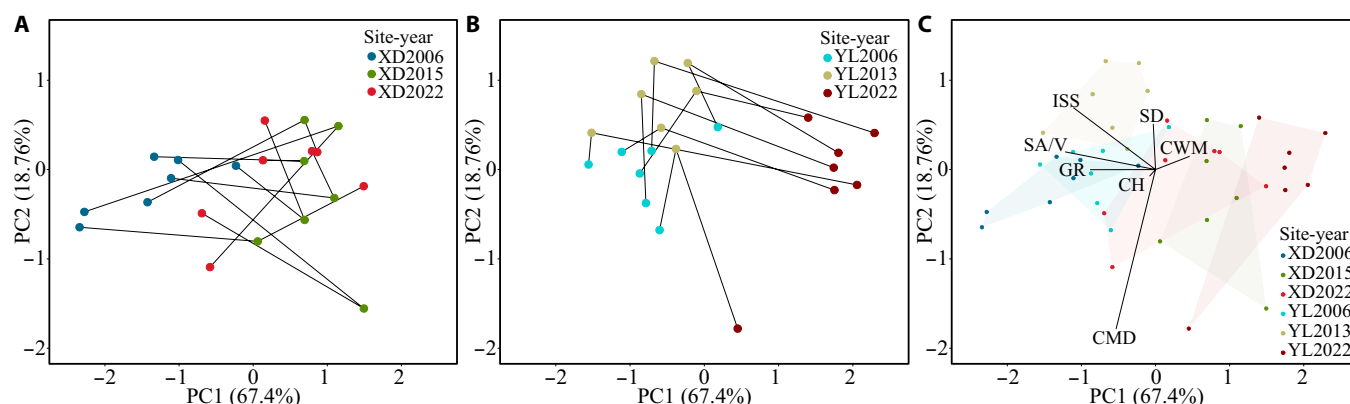


Fig. 4. Functional trajectories of coral communities in the Xisha Islands from 2006 to 2022. Blue dots indicate the start of the successional trajectory, and red dots indicate the final time of the successional trajectory. (A) Xuande Atoll. (B) Yongle Atoll. (C) Contribution of coral traits to the principal components analysis (PCA) axis and the trait vectors are skeletal density (SD), surface-area-to-volume ratio (SA/V), growth rate (GR), interstitial space size (ISS), colony maximum diameter (CMD), colony height (CH), and corallite width maximum (CWM).

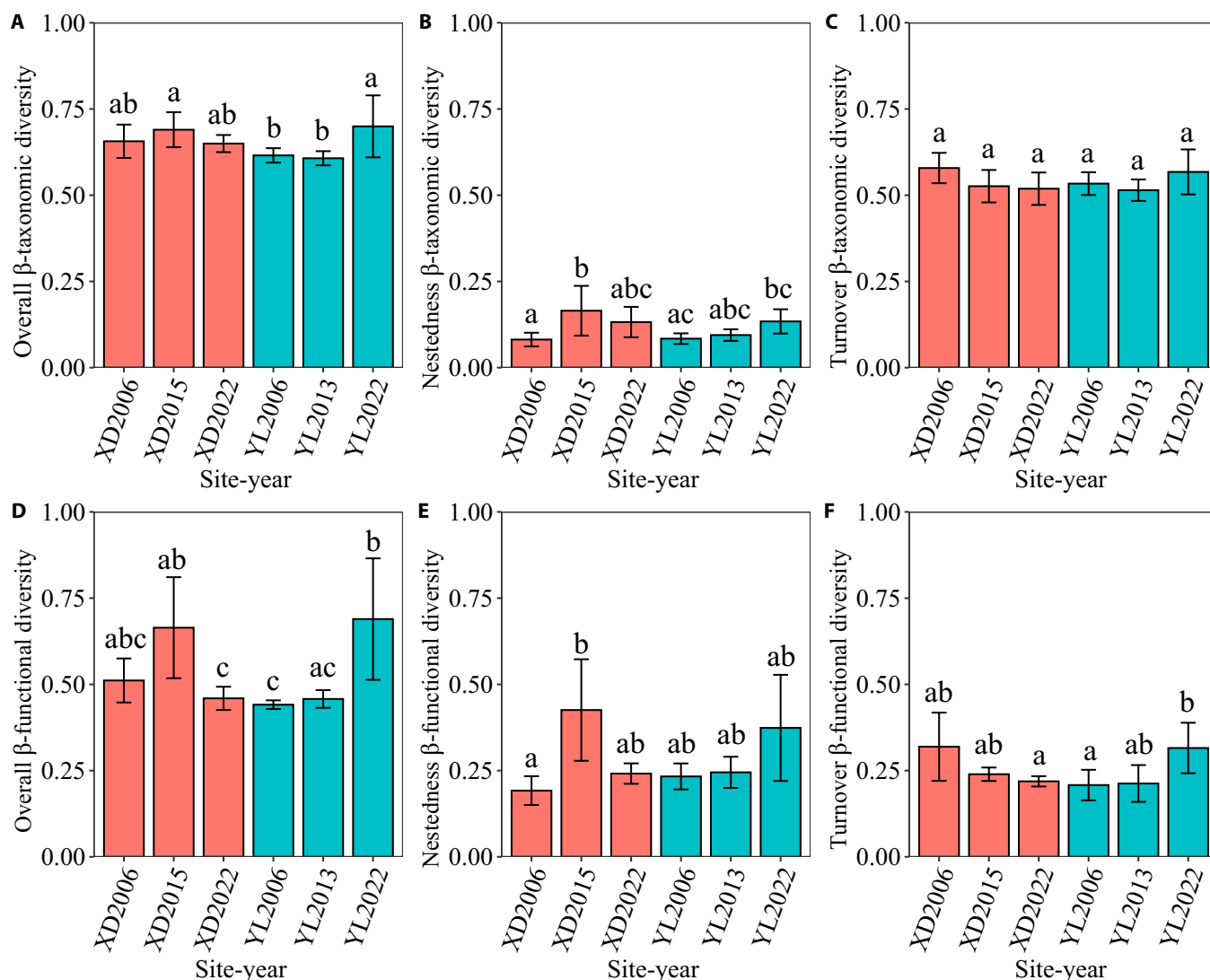


Fig. 5. Communities β -diversity parameters variation in the Xisha Islands from 2006 to 2022. (A) Overall β -taxonomic diversity. (B) Nestedness β -taxonomic diversity. (C) Turnover β -taxonomic diversity. (D) Overall β -functional diversity. (E) Nestedness β -functional diversity. (F) Turnover β -functional diversity. Letters are labeled as Dunn test results.

corals are primarily branching corals, the decline in *Acropora* biomass is also reflected in the trajectory of functional trait changes. From a functional perspective, species with higher growth rates, larger surface-area-to-volume ratios, and greater spatial complexity were lost, while species with larger corallite sizes became dominant.

Recurrent disturbances may further exacerbate the degradation of already impacted communities. Following another outbreak of CoTS in 2022, coral cover in Yongle Atoll declined further, accompanied by a significant decrease in functional diversity. The degradation trajectory of this community showed a strong directional trend in both community structure and functional traits, evolving toward lower coral cover and a reduced presence of structurally complex corals [20,24]. Meanwhile, both β -taxonomic and β -functional diversity exhibited an increasing trend at Yongle Atoll, while the turnover component did not decrease but rather increased. This indicated that the degradation of the coral community was evolving, to a certain extent, not toward homogenization but toward diversification. Our results differ from other research findings, where multiple studies indicated that degradation leads to increased nestedness, while

species turnover remains stable or even declines [39,40]. This occurs because during degradation, generalist and tolerant species replace other species within the community [20,41]. However, during severe outbreaks of CoTS, CoTS consume all available coral, including species that might otherwise be considered lower-priority prey [15,42], which may be associated with the diversification of degraded communities here. Moreover, this diversification occurred against a backdrop of reduced α -taxonomic diversity and -functional diversity, meaning that species and functional compositions at individual sites were likely more simplified than anticipated. It emphasizes that in assessing the dynamics of community degradation and recovery, both spatial and temporal variations in β -diversity and -functional diversity must be considered concurrently [40]. Although thermal stress events occurred during the study period, the temporal correspondence between the second CoTS outbreak at Yongle Atoll and the subsequent sharp decline in coral cover suggests that this outbreak represented a major disturbance event. At the same time, the recurring thermal stress following the initial outbreak likely contributed alongside the second outbreak to the ongoing degradation of Yongle Atoll. Under such cumulative thermal

pressures, repeated outbreaks may increase the likelihood of communities shifting toward simplified and functionally reduced states. Therefore, controlling the frequency of CoTS outbreaks is essential to prevent the shift toward a simplified, degraded state of coral reefs.

Coral community recovery and limitations after the outbreak of CoTS

The degradation of community structure and functional traits in Yongle Atoll appears to be less pronounced following the 2006 outbreak compared to Xuande Atoll according to the community's data from 2013 to 2015. However, monitoring results from other studies indicated that both atolls experienced significant degradation following the 2006 CoTS outbreak [26,28]. Therefore, we speculated that Yongle Atoll is not less degraded but rather in a state of recovery from degradation. Evidence in support of this speculation can be seen in the change in community structure, where the dominant species in Yongle Atoll shifted from the staghorn coral *Acropora* in 2006 to *Pocillopora* coral in 2013. Studies in other regions have also shown that *Pocillopora* acts as a pioneer species in coral community recovery [43]. Therefore, the rapid proliferation of *Pocillopora* was responsible for the recovery of coral cover and functional trait structure after degradation.

The rate of coral communities recovery after disturbance such as CoTS outbreaks is influenced by disturbance frequency, and the condition of the surviving community after degradation, meaning that the time required to regain original coral cover can range from 5 to 100 years [10]. In the Indo-Pacific Ocean, large-scale CoTS outbreaks occurred between the 1950s and 1960s, but by the 1980s, coral reefs had returned to their preoutbreak conditions [44]. Recent monitoring in several reef regions has also documented coral community recovery after CoTS outbreaks [45]. Despite marine heatwaves during the period 2013–2022, coral cover in Xuande Atoll has been slowly recovering after the CoTS outbreak. Compared to the rapid recovery of cover at Yongle Atoll in 2013, Xuande Atoll showed a lower level of coral cover in 2015, which may be related to thermal stress events. Previous studies have shown that abnormal seawater temperatures can lead to coral bleaching and death, which, in turn, leads to a decline in coral cover [22]. In fact, according to survey data from other studies, the coral cover of Xisha Islands remained below 10% between 2011 and 2018 and only began to show a recovery in cover after 2019 [26]. The timing of the cover recovery coincided with the disappearance of the heat stress event. It is therefore reasonable to speculate that the heat stress event substantially inhibited coral cover recovery after the Xisha Islands CoTS outbreak. However, our data do not allow for a full quantitative disentanglement of the relative impacts of CoTS outbreaks versus concurrent thermal stress. In the absence of site-specific, time-aligned data on CoTS densities, we interpret the observed community changes as likely driven by the compounding effects of these disturbances. While CoTS outbreaks are strongly implicated in the initial phase of coral decline, a more cautious and inclusive interpretation points to the cumulative pressure from both postpredation status and intermittent thermal stress as shaping the slow recovery trajectories observed at Xuande Atoll.

Community recovery must be considered at multiple levels, as the recovery patterns of species richness, species composition, and functional diversity differ [46]. The recovery trajectory of coral community structure and functional traits indicated that

Xuande Atoll was gradually returning to its predegradation state. In particular, species richness and functional diversity have nearly recovered to its predisturbance level, suggesting that the recovering species were not concentrated within a single functional trait group but include species from different functional categories. However, the community and functional trait structure of Xuande Atoll has not fully returned to its 2006 state. Notably, the cover and diversity of corymbose and table/plate coral species have not yet recovered, which aligns with their extremely low biomass in 2015. As of 2022, the dominant coral group in Xuande Atoll remains the massive growth form, indicating that certain functional groups are still missing in the recovery process, consistent with findings from other studies [6,47]. It is worth noting that these key groups lacking recovery are both preferred prey for CoTS and sensitive to thermal bleaching. It is likely this combined vulnerability that has prevented them from recovering their biomass during the intermittent thermal bleaching events following the starfish outbreaks. Thus, although CoTS is a naturally occurring predator whose grazing may help regulate coral community structure under healthy reef conditions, the observed postoutbreak recovery—including a slight increase in species diversity—should not be interpreted as evidence of beneficial regulation by CoTS. This is particularly relevant given the severe, multilevel biodiversity declines during the CoTS outbreak phase, coupled with the ongoing disruption anticipated from climate change in the future [10,12,13,37]. Consequently, in future scenarios characterized by frequent disturbances, coral reefs, similar to many other ecosystems, face the risk of certain functional groups failing to recover [3,48]. Therefore, future coral reef conservation and management efforts should prioritize the protection of these vulnerable species.

Conclusion

Overall, our long-term monitoring in the Xisha Islands indicated that CoTS outbreaks were closely associated with rapid degradation of coral cover and functional diversity. A single severe outbreak at Xuande Atoll demonstrated that recovery is possible: Coral cover, species richness, and functional diversity at some sites returned to predisturbance levels after 16 years, despite intermittent thermal stress inhibiting the rate of recovery. However, this recovery was slow, lagging significantly for structurally complex corals (e.g., corymbose and table corals), and was further impeded by seawater temperature anomalies. In contrast, a second CoTS outbreak at Yongle Atoll alters this recovery trajectory under continued thermal stress. It was associated with reductions in coral cover and a shift toward a community increasingly dominated by structurally simpler species. Notably, while overall biodiversity declined, the variation among communities increased, indicating that recurrent disturbance leads to both a broad “simplification” and a localized “diversification”. In a future of increasing disturbances, such repeated perturbations pose a severe challenge to reef resilience. Therefore, effective conservation must not only focus on protecting sensitive functional groups but also prioritize mitigating the frequency of acute disturbances, including recurrent CoTS outbreaks and interacting stressors. Key management priorities include establishing early-warning and rapid-response programs to control initial outbreaks, as well as implementing targeted measures—such as spatial refuges or active restoration—to safeguard structurally complex, recovery-sensitive corals such as corymbose and table species. It is also crucial to integrate CoTS outbreak

mitigation into broader climate-adaptive management frameworks to reduce cumulative stressors. As climate-driven thermal anomalies become more frequent, the interaction between biological disturbances and heat stress may increasingly determine reef recovery potential. Collectively, the evidence presented here supports the development of adaptive, evidence-based strategies aimed at preserving the structural and functional integrity of coral reefs amid escalating disturbances.

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Data Availability

The data associated with the article have been archived in the Science data bank (<https://www.scidb.cn/anonymous/QUpqVWpl>)

Supplementary Materials

Figs. S1 to S3

Table S1

References [49,50]

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Ecosystem Health and Sustainability

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Recurrent Crown-of-Thorns Starfish (*Acanthaster cf. solaris*) Outbreaks Alter Coral Recovery Trajectories in the Central South China Sea

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Tracking the degradation and recovery of foundational organisms is key to understanding ecosystem sustainability. Using coral reefs as a model, we investigated how disturbance frequency affects the recovery of reef-building corals. We examined changes in coral cover, #- and #-taxonomic diversity, functional diversity, and community structure over 3 periods (2006, 2013–2015, and 2022) across 14 sites on 2 atolls in the central South China Sea, where crown-of-thorns starfish outbreaks occurred at different frequencies. Building on 2006 baseline surveys prior to crown-of-thorns starfish-induced decline, our 2013–2015 assessments captured early postoutbreak structural recovery alongside localized degradation associated with thermal stress. Recurrent outbreaks at Yongle Atoll were associated with further community degradation, with communities shifting toward dominance by structurally simpler species. Despite a decline in the overall species and functional composition of communities, #-diversity decomposition revealed that coral communities retained a trend toward functional diversification after repeated outbreaks, meaning that species and functional compositions at individual sites are likely more simplified than anticipated. At Xuande Atoll, which experienced only one major outbreak, coral cover, species richness, and functional diversity at some sites recovered to predisturbance levels within 16 years, despite intermittent thermal stress inhibiting the rate of recovery. However, community structure recovery lags behind, as the delayed recovery of structurally complex groups (e.g., corymbose and table corals) constrains the overall community recovery. Overall, while coral communities can demonstrate recovery potential, repeated disturbances disrupt this process. Therefore, effective conservation must focus on protecting sensitive functional groups and mitigating the frequency of disturbances.

Image

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