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The effects of coral assemblage shift on reef functions in Akumal, Mexico

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ABSTRACT: Caribbean coral reefs have suffered shifts in their coral assemblages, driven by local and global stressors. These shifts have affected reef functions, ecosystem processes, and services essential to human well-being. Akumal Reef, located in the northern Mexican Caribbean, generates valuable ecosystem services, mainly linked to tourism, that depend on the persistence of the reef's physical functionality. In this study, decadal changes in coral assemblages and their effects on functional traits decline were investigated. Coral species cover was systematically monitored at 14 sites along Akumal Reef in 2001, 2010, and 2019. These data were translated to functional traits allowing the classification of coral species into life-history strategies (competitive, stress-tolerant, and more opportunistic 'weedy' species). Our results indicate a significant decline in stress-tolerant species cover (mostly from the genus *Orbicella*) in Akumal Reef between 2001 and 2010 and between 2010 and 2019, with no significant changes in coral cover of other life-history strategies. The significant shifts away from stress-tolerant species during the time studied in Akumal Reef influenced the deterioration of functional traits related to reef physical functionality, such as calcification, rugosity, average maximum colony size, and reef functional index. Currently, Akumal reef sites are dominated by non-framework-building weedy coral species and are mostly below the 10% hard cover estimated threshold for positive reef accretion in the Caribbean. Therefore, management strategies in Akumal Reef should be integrative and oriented towards reducing local stressors while actively restoring the functional structure of coral reefs and maintaining their environmental services.

KEY WORDS: Akumal reef · Coral life-history strategies · Coral functional traits · Reef functional index

1. INTRODUCTION

Since the 1950s, Caribbean coral reefs have experienced major benthic changes, with an overall decline in coral cover, coupled with an increase in macroalgae cover (Gardner et al. 2003, Jackson et al. 2014, Cramer et al. 2019). Moreover, significant coral assemblage shifts have also been reported in the Caribbean, describing, for example, the decline of structurally complex fast-growing species and their replacement by plate species (Green et al. 2008, Alvarez-Filip et al. 2011). These shifts in coral assemblages may translate into changes in Caribbean coral reef function (Perry & Alvarez-Filip 2019), which in turn affect ecosystem processes and services essential to human well-being (Mumby et al. 2007, Jackson et al. 2014, Hughes et al. 2017).

Indeed, ecosystem functions and services largely depend upon the combination of species and traits that form biological assemblages (Mouillot et al. 2013), particularly in the case of engineer species such as hard corals. Thus, a functional trait-based approach is the most relevant to quantify, predict, and better anticipate ecological assemblages' responses to natural or anthropogenic disturbances (Mouillot et al. 2013) and to support relevant man-

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agement decisions (Leitao et al. 2016). Multi-trait studies based on ecological principles enable the simplification of functional space complexity in synthetic axes. This allows species to be clustered based on these traits and those with unique combinations of traits to be identified (Mouillot et al. 2021).

Currently, systematized information on many corals traits is available (Madin et al. 2016, McWilliam et al. 2018). This allows the classification of species into life-history strategies (Darling et al. 2012, 2019) and an understanding of changes in reef processes such as resistance and recovery, as well as reef functions such as reef growth and habitat provision (Randazzo-Eisemann et al. 2021a). Particularly in the Caribbean, there has been a growing interest in understanding shifts in reef physical functionality through coral traits studies (González-Barrios & Álvarez-Filip 2018, Estrada-Saldívar et al. 2020, González-Barrios et al. 2021, Melo-Merino et al. 2022) due to the high susceptibility to anthropogenic global and local stressors that this region has been facing for more than 5 decades (Jackson et al. 2014). These studies have been focused on guiding efforts to preserve coral reef functionality and define priority conservation areas in the Caribbean.

For instance, the Caribbean has been described as a functionally depauperated coral region, with ~65% of coral species having unique trait combinations, and thus only ~35% functional redundancy (McWilliam et al. 2018). Coral species from the genera *Acropora*, *Orbicella*, and *Dendrogyra* — which have a major contribution to reef growth and habitat provision — are functionally unique, and their abundance is decreasing in the region (Alvarez-Filip et al. 2009). These genera have been impacted by coral disease outbreaks: white band disease affecting *Acropora* spp. (Aronson & Precht 2001), yellow band disease impacting mainly *Orbicella* spp. (Edmunds & Elahi 2007), and stony coral tissue loss disease (SCTLD) causing local extinctions of *Dendrogyra cylindrus* and gravely affecting dozens of other species (Precht et al. 2016, Precht 2021). Consequently, the lack of functional redundancy in Caribbean coral species potentially homogenizes the response of coral assemblages to stressors and compromises the resilience of this coral province (McWilliam et al. 2020).

Akumal Reef, located in the north of Quintana Roo, Mexico, was the first tourist destination of the Mexican Caribbean coastal fringe (Aranda-Fragoso 2016). Early scientific studies from the late 1970s and the 1980s described the northern portion of Quintana Roo's reefs as dominated by highly diverse scleractinian coral assemblages (Jordán-Dahlgren 1979, Zlatarski 2007). Akumal Reef's first quantitative assessments in the 1990s mentioned a coral cover estimated between 25 and 54%, with a dominance of *Orbicella annularis*, while macroalgae coverage was estimated at between 27 and 46% of the substrate (Jordán-Dahlgren 1993, Gutiérrez-Carbonell et al. 1995). However, the system has experienced a gradual but important degradation over the last 3 decades, related to the increasing impact of local and global stressors (Molina-Hernández et al. 2018, Randazzo-Eisemann et al. 2021b). Since the late 1990s, Akumal Reef has been systematically monitored, providing a case study to quantify functional decadal changes in coral reefs (Fig. 1).

Local stressors affecting Akumal Reef are associated with the lack of a sustainable coastal development plan, and more precisely, the negative conse-

Fig. 1. Monitoring of Akumal Reef decadal changes in 2000, 2010, and 2019, illustrating reef degradation through changes in benthic cover. In 2001, note the remnants of a luxuriant *Acropora cervicornis* cover, and *Orbicella annularis* live cover (yet with some diseases present). In 2010, agariciids played a more relevant role in coral cover while some standing-dead *Acropora palmata* colonies contributed to the reef framework, and in 2019 the coral cover contribution is mainly given by smaller coral colonies

quences of an accelerated urban expansion driving direct habitat destruction (Molina-Hernández et al. 2018), land-based pollution (Hernández-Terrones et al. 2011), and overfishing (Roy 2004). In addition to these chronic local stressors, since the late 1990s, Akumal has been impacted by more frequent and intense acute stressors (Randazzo-Eisemann et al. 2021b), such as bleaching events (in 1998, 2005, 2010, 2014–2017, and 2019) and disease outbreaks (white plague in 1998, yellow band disease in 2010, and SCTLD in 2018).

In this study, we hypothesize that in the last 2 decades, coral assemblage shifts translated directly into the incapacity of the remaining coral species to maintain the reef's physical functionality. To assess this hypothesis, coral species identified in Akumal Reef in 2001, 2010, and 2019 were grouped into 3 existing coral life-history strategies (competitive, stress-tolerant, and weedy) with different framework-building capacities. Decadal changes in the abundance of the 3 coral life-history strategies and in quantitative values of functional traits were evaluated. Finally, the links between changes in coral assemblages and the reef's physical functionality were examined.

2. MATERIALS & METHODS

2.1. Study area

The study area is Akumal Bay, located in the northern Mexican Caribbean (Fig. 2), extending from Sirenis Bay in the north to X'Cacel in the south. Along this area, 14 GPS-marked reef sites, which were systematically monitored in 2001, 2010, and 2019, were selected, of which 7 are on the front reef, and 7 are on the reef slope.

2.2. Data collection

2.2.1. Coral cover per species

For each of the 14 selected sites and each monitoring campaign (2001, 2010, and 2019), reef benthos was recorded with a high-resolution camera in a 30 m^2 (50 × 0.6 m) non-permanent transect, maintaining the video at a constant 0.4 m height throughout the transect (Garza-Pérez 2004). To estimate benthic cover percentage, 40 evenly spaced freeze-frames in each video were sub-sampled, and for each frame, 13 points systematically positioned on the screen were associated with a specific benthic category such as macroalgae, turf algae, or sponge, while live corals were identified to species level. For each benthic category and coral species, a percentage based on the total 520 points per site was calculated. For this study, only coral cover per species data was used.

2.2.2. Coral traits

Four major reef ecosystem functions and processes — reef growth, habitat provision, resistance, and recovery — were associated with 7 different coral species traits: (1) calcification rate, (2) maximum colony size, (3) colony growth form, (4) rugosity, (5) corallite maximum size, (6) reproductive mode, and (7) depth range (Table S1 in the Supplement at www.int-res.com/articles/suppl/m695p053_supp.pdf). These quantitative and qualitative traits

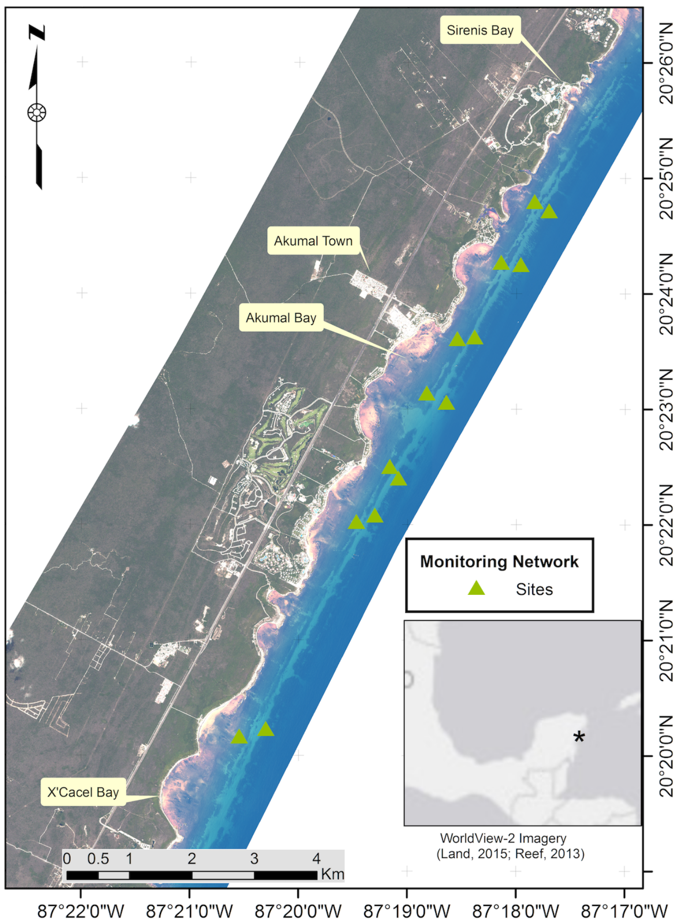

Fig. 2. Satellite photo of the study area: Akumal Reef, located in the northern Mexican Caribbean, encompassing the zone from Sirenis inlet (north) to X'Cacel (south). The reef sites are symbolized by green triangles, with representation from both the front reef and slope

were selected as there is accurate information for all Caribbean coral species, and they allow coral species to be grouped in 3 life-history strategies based on Darling et al. (2012) and Randazzo-Eisemann et al. (2021a).

Trait information was collected for a total of 40 scleractinian corals identified at the sites in 2001, 2010, and 2019 (Table S2). The information for maximum colony size, corallite maximum size, depth range, and reproductive mode was retrieved from the coral trait online database (Madin et al. 2016) and was completed and verified using various sources such as regional identification books (Humann & DeLoach 2002, Charteris 2017). The information for calcification rate, rugosity, and colony growth form was obtained from González-Barrios & Álvarez-Filip (2018).

Additionally, to analyze changes in Akumal reef physical functionality between 2001, 2010, and 2019, the functional coefficient (*Fc*), calculated as the average of standardized calcification, rugosity, and mean colony height, was obtained for all 40 coral species from González-Barrios & Álvarez-Filip (2018).

2.3. Data analyses

Following Randazzo-Eisemann et al. (2021a), the 40 species detected were grouped into 3 life-history strategies (competitive, stress-tolerant, and weedy) through a principal coordinates analysis (PCoA) (Mouillot et al. 2013) using Gower's dissimilarity, as this allows for a comparison of mixed data types, can handle missing values, and can weight individual traits differently (Laliberté & Legendre 2010). This analysis was performed using the R packages ade4, ape, and ggplot2 (R Core Team 2022).

The coral cover per life-history strategy per site was plotted to evaluate coral cover decadal changes, taking as a reference the estimated threshold value of 10% total coral cover. This represents the minimum hard coral cover necessary for positive accretion estimated for Caribbean coral reefs (Perry et al. 2013). The statistical differences between the coral cover per life-history strategy per campaign were tested through a non-parametric Wilcoxon text. Analysis was performed using the R packages ggplot2, ggpubr, and gridExtra (R Core Team 2022).

For each campaign, the potential calcification rate (Eq. 1) per site was estimated through the summation of the product of the cover of each coral species and its calcification rate, divided by the transect area (30 m^2). In the case of rugosity (Eq. 2) and maximum colony size (Eq. 3), averages per site were obtained, through the summation of the product of the cover of each coral species and its trait value, divided by the total site coral cover. The reef functional index (RFI; Eq. 4) was calculated following González-Barrios & Álvarez-Filip (2018):

$$\mathrm{Cal}_{sy} = \frac{\sum_{i=1}^{n} \mathrm{LC}_i \times \mathrm{MaxS}_i}{30} \quad (1)$$

$$\mathrm{Rug}_{sy} = \frac{\sum_{i=1}^{n} \mathrm{LC}_i \times \mathrm{Rug}_i}{\mathrm{LC}_S} \quad (2)$$

$$\mathrm{MaxS}_{sy} = \frac{\sum_{i=1}^{n} \mathrm{LC}_i \times \mathrm{MaxS}_i}{\mathrm{LC}_S} \quad (3)$$

$$\mathrm{RFI}_{sy} = \frac{\sum_{i=1}^{n} \mathrm{LC}_i \times \mathrm{Fc}_i}{100} \quad (4)$$

where Cal_{sy} is the potential calcification rate at a given site *s* for a given year *y*. Rug_{sy} and MaxS_{sy} are average rugosity and maximum size, respectively, at a given site *s* for a given year *y*. RFI_{sy} is the reef functional index at a given site *s* for a given year *y*. $\mathrm{LC_i}$ is the cover for a given coral species *i*. Cal_i, Rug_i, MaxS_i, and Fc_i are calcification, rugosity, maximum size, and the functional coefficient, respectively, for a given coral species *i*. The potential calcification rate, the average rugosity and maximum size, and RFI were box-plotted by campaign year, and the statistical differences were tested through a non-parametric Wilcoxon text. This analysis was performed using R libraries ggplot2, ggpubr, and gridExtra (R Core Team 2022).

Finally, a general linear model (GLM) incorporating a Gaussian distribution was performed to explain the RFI as a function of competitive, stress-tolerant, and weedy species cover. Each main factor's effect was represented using a partial regression plot, which estimates the relationship between each factor and the predicted variable while holding other factors constant at their medians. This analysis was performed using the R packages ggplot2 and visreg (R Core Team 2022).

3. RESULTS

The functional space based on the 7 traits selected allows the 40 coral species identified to be classified into 3 life-history strategies (Fig. 3). Each life-history strategy is characterized by particular functional traits: competitive coral species are branching frame-

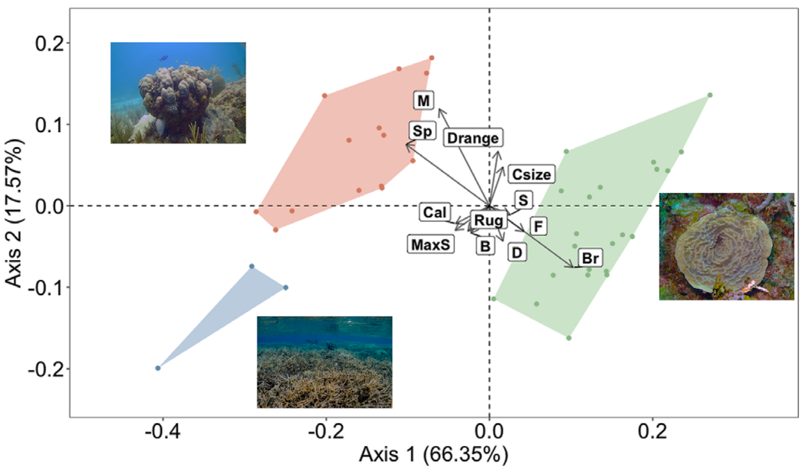

Fig. 3. Principal coordinates analysis (PCoA) showing the functional space components (1 and 2), representing the distribution of the 40 coral species identified in Akumal Reef in 2001, 2010, and 2019, according to 7 functional traits. The traits considered were colony growth form (B: branching; D: digitate; F: foliose; M: massive; S: sub-massive), rugosity (Rug), calcification rate (Cal), maximum colony size (MaxS), reproduction (Br: brooders; Sp: spawners), corallite maximum size (Csize) and depth range (Drange). The colors represent life-history strategies: blue for competitive species, orange for stress-tolerant species, and green for weedy species

work builders (high calcification rates, high rugosity, and large size) and spawners; stress-tolerant taxa are massive framework builders (low calcification rates, high rugosity, and large size) and spawners; and weedy taxa are mostly non-framework builders and brooders (Fig. 3).

In 2001, all sites were above 10 % hard coral cover (Fig. 4a), corresponding to the estimated threshold of positive reef accretion in the Caribbean (sensu Perry et al. 2013). While framework-builder competitive coral species already had low cover at the beginning of this study, coral assemblages were still dominated by framework-builder stress-tolerant coral species at most of the sites (Fig. 4a). Between 2001 and 2010, live coral declined in Akumal Reef, and by the end of this period 64 % of the sites were below 10 % hard coral cover, and all coral life-history strategies were less abundant (Fig. 4b). Between 2010 and 2019, the loss of hard coral cover continued, with an additional 15 % of the sites falling below 10 % hard coral cover (for a total of 79 % of sites), and the stress-tolerant coral species exhibiting the greatest loss in cover (Fig. 4c, and Tables S3–S5). The cover of stress-tolerant coral species was the only one that decreased significantly ($p < 0.05$) among the 3 life-history strategies, for both periods 2001–2010 and 2010–2019 (Fig. 4d–f), with a clear significant effect ($p < 0.05$) in the trend of a decrease in total coral cover between 2001 and 2010 (Fig. S1).

The potential calcification rate, average rugosity, and RFI decreased significantly ($p < 0.05$) between 2001 and 2010, with no significant signs of recovery between 2010 and 2019 (Fig. 5a,b,d). The theoretical average maximum coral size (associated with the existing coral species assemblage) did not change significantly between 2001 and 2010, but a significant decrease ($p < 0.05$) was observed between 2010 and 2019 (Fig. 5c).

The average RFI in Akumal Reef, which integrates the traits associated with framework building (calcification, rugosity, and colony size), was significantly predicted ($p < 0.05$) by both competitive and stress-tolerant coral species but was not strongly related to weedy species cover in Akumal Reef (Fig. 6 and Table 1). Partial relationships show that the RFI was positively related to competitive and stress-tolerant species cover (Fig. 6a,b) and slightly negatively related to weedy species cover (Fig. 6c).

4. DISCUSSION

The present study highlights decadal changes in coral assemblages in Akumal Reef and the impact of these shifts on reef physical functionality. At the beginning of the study in 2001, competitive coral cover was already low, yet stress-tolerant cover was high and these species were a dominant component of the coral assemblages. Our results indicate a significant decline in stress-tolerant species cover in Akumal Reef between 2001 and 2010, and again between 2010 and 2019, with no significant changes in coral cover of other life-history strategies, indicating that competitive species from the genera *Acropora* and *Dendrogyra* have not shown significant recovery, and opportunistic species from the genera *Agaricia* and *Porites* remain stable, despite multiple stressors affecting Akumal. The significant shifts in stress-tolerant species during the study period in Akumal Reef influenced the decline of functional traits related to reef physical functionality, such as calcification, rugosity, average maximum size, and RFI.

Species turnover in coral assemblages has been described in the Caribbean at the regional level since the 1980s (Aronson et al. 1998, Aronson et al. 2002),

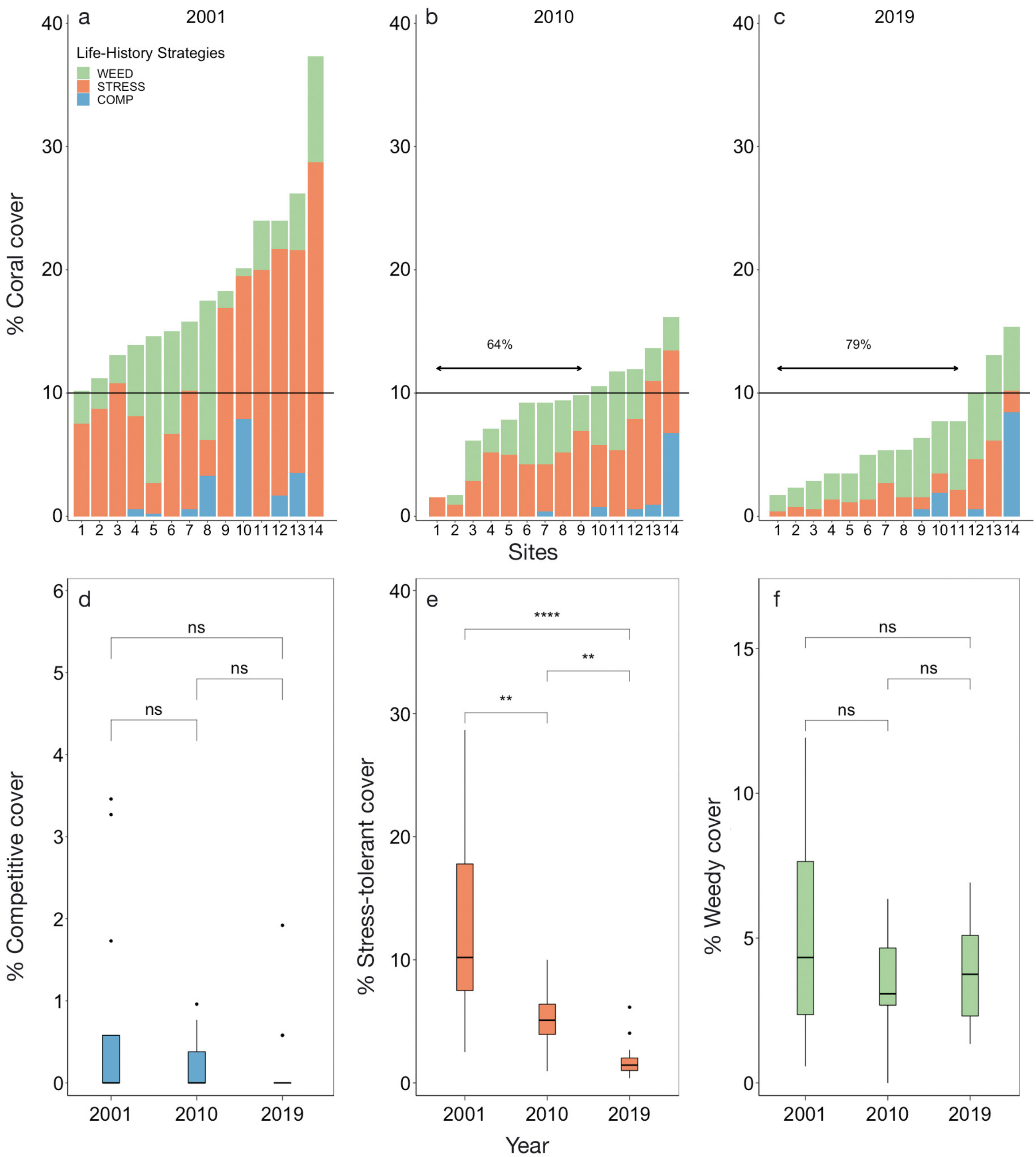

Fig. 4. Coral cover (from lowest to highest) along the 14 sites surveyed in (a) 2001, (b) 2010, and (c) 2019. The percent cover of competitive species is represented in blue, stress-tolerant species in orange, and weedy species in green. The percentage of sites with <10% hard coral cover is noted above the black arrow in b and c. Live changes between 2001, 2010, and 2019 for each life-history strategy: (d) competitive, (e) stress-tolerant, and (f) weedy are represented using boxplots (box: interquartile values; horizontal line: median: whiskers extend to one and a half times the interquartile range; points: outliers). Statistical significance between the year boxplots is indicated (ns: $p > 0.05$, $^*p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$, and $^{****}p \le 0.0001$)

when white band disease decimated 80 to 98% of *Acropora* spp. populations (Kline & Vollmer 2011). Since then, the lack of recovery of competitive corals has resulted in a flattening of Caribbean coral reefs (Alvarez-Filip et al. 2009). This regional trend of declining architecture coincides with other key acute regional disturbances in recent Caribbean ecological history: the mass mortality of the grazing sea urchin *Diadema antillarum* that facilitated macroalgae growth, and the 1998 El Niño–Southern Oscillation-induced worldwide coral bleaching event that mostly affected structurally complex coral species (Alvarez-

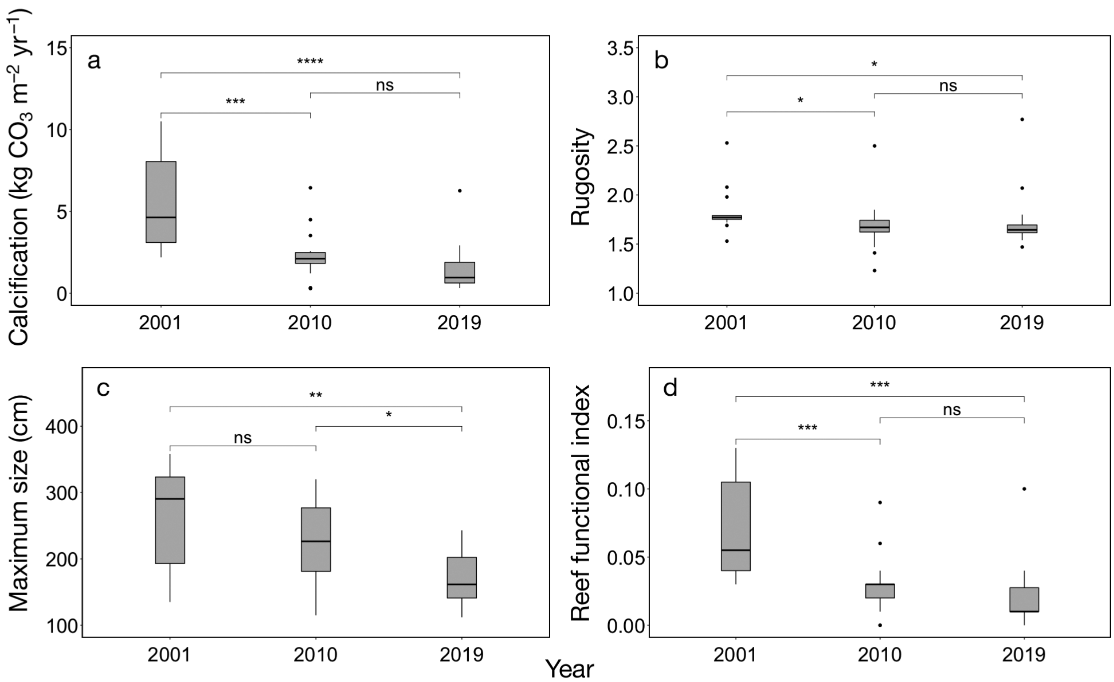

Fig. 5. Boxplots of functional trait change between 2001, 2010, and 2019 in (a) calcification rates per site, (b) rugosity per site, (c) average maximum coral size per site, and (d) average reef functional index per site in Akumal Reef. The box represents the interquartile values, the horizontal line the median, the whiskers extend to one and a half times the interquartile range, and the points are considered outliers. Statistical significance between the year boxplots is indicated (not significant, ns: $p > 0.05$, $^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$, and $^{****}p \leq 0.0001$)

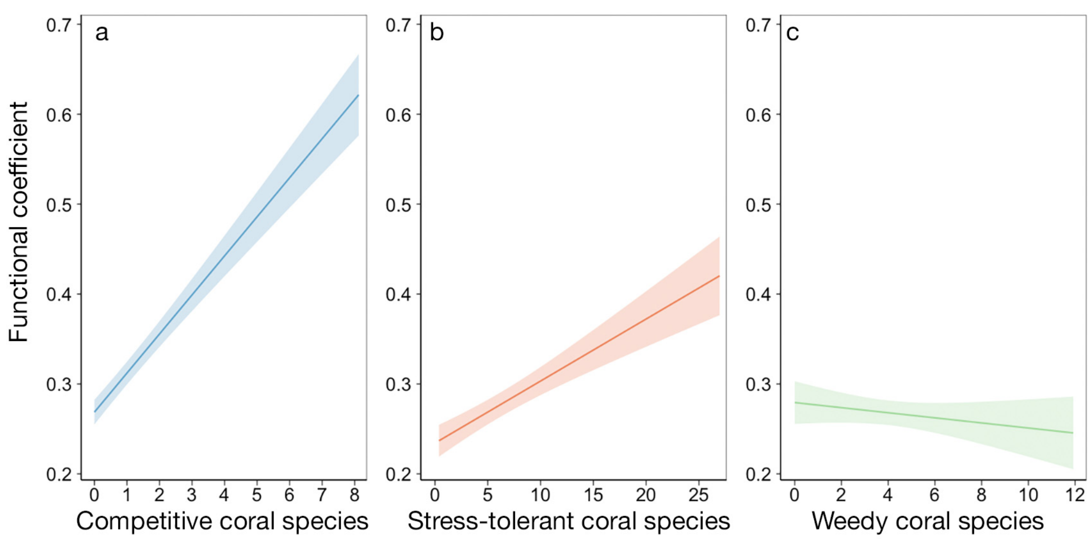

Fig. 6. Generalized linear model (GLM) of the average reef functional index in Akumal Reef as a function of (a) competitive coral species cover, (b) stress-tolerant coral species cover, and (c) weedy coral species cover. The *y*-axis displays the partial residuals of functional coefficient as a function of each of the factors retained in the final model, conditioned on the median value of all other retained factors. The shading represents the 95 % confidence interval for the partial residuals curve

Filip et al. 2009). More recently, the accelerated accumulation of heat stress levels has triggered more intense and frequent bleaching events (Skirving et al. 2019). Emergent lethal coral disease outbreaks such as SCTLD (Precht 2021) also continue to negatively impact coral cover in the Caribbean, profoundly impacting coral functionality (Perry et al. 2015, Estrada-Saldívar et al. 2019, Courtney et al. 2020). For instance, in the first 2 yr of the SCTLD outbreak (2018–2019), Akumal Reef lost almost half of its remaining coral cover (Randazzo-Eisemann et al. 2021b).

Table 1. Summary of the model terms and statistical values. ***p ≤ 0.001

Terms	Estimate	SE	t	p
Intercept	0.245	0.013	18.536	<2e–16***
Competitive	0.043	9.436	12.24	<2e–16***
Stress-tolerant	0.007	0.001	6.791	4.72e–08***
Weedy	–0.003	0.002	–1.154	0.256

The lack of recovery of Caribbean coral assemblages in terms of species and cover might be explained by both external factors and internal ecosystem dynamics acting upon the reefs over the past 2 decades. External factors represent the increase of both chronic (pollution and overfishing) and acute (bleaching events, disease outbreaks, hurricanes, physical damages) stressors and their cumulated interactions (Arias-González et al. 2017, Suchley & Alvarez-Filip 2018). Internal ecosystem dynamics can be associated with feedbacks that prevent recovery: (a) lower rates of coral recruitment (Mumby et al. 2014); (b) inhibition as a result of inter-species competition (Randazzo-Eisemann et al. 2019); (c) the decline of response diversity due to loss of functional traits and low functional redundancy (Biggs et al. 2015, McWilliam et al. 2020); and (d) crossing key ecosystem thresholds (Fung et al. 2011). For example, a key threshold for coral reefs is to reach the state of accretionary stasis (sensu Perry et al. 2013), meaning that reefs with low calcification are transitioning to negative carbonate budget states, lowering reef carbonate production rates, potentially impairing reef growth, and ultimately leading to net reef erosion (Perry et al. 2015, Molina-Hernández et al. 2020).

In this same regional context, but at a smaller scale, Akumal Reef has been facing increased chronic and more frequent and intense acute stressors in the last 2 decades (Fig. 7) in the form of poorly planned urban development, bleaching events, and disease outbreaks (Contreras-Silva et al. 2020, Randazzo-Eisemann et al. 2021b). Thus, coral cover has declined, total algae cover has increased (Randazzo-Eisemann et al. 2021b), and this algae-dominant regime is maintained by internal positive feedbacks such as competitive inhibition and lack of coral recruitment. The shifts in coral assemblages from 2001 to 2019, leading to reef sites dominated by non-framework building small weedy coral species, have resulted in a low contribution to reef physical functionality and are mostly below the 10% estimated threshold for reef positive accretion in the Caribbean. Consequently, the lack of recovery observed in Akumal Reef between 2001 and 2019 might therefore be the overall result of the cumulative effects of increased stressors and algae, poor reef accretion, and the overall decrease in functional traits and the potential response diversity of the system.

Nevertheless, Akumal is still one of the most popular tourist sites in the Mexican Caribbean, conveniently located between Playa del Carmen and Tulum. Its economy is highly dependent on coral

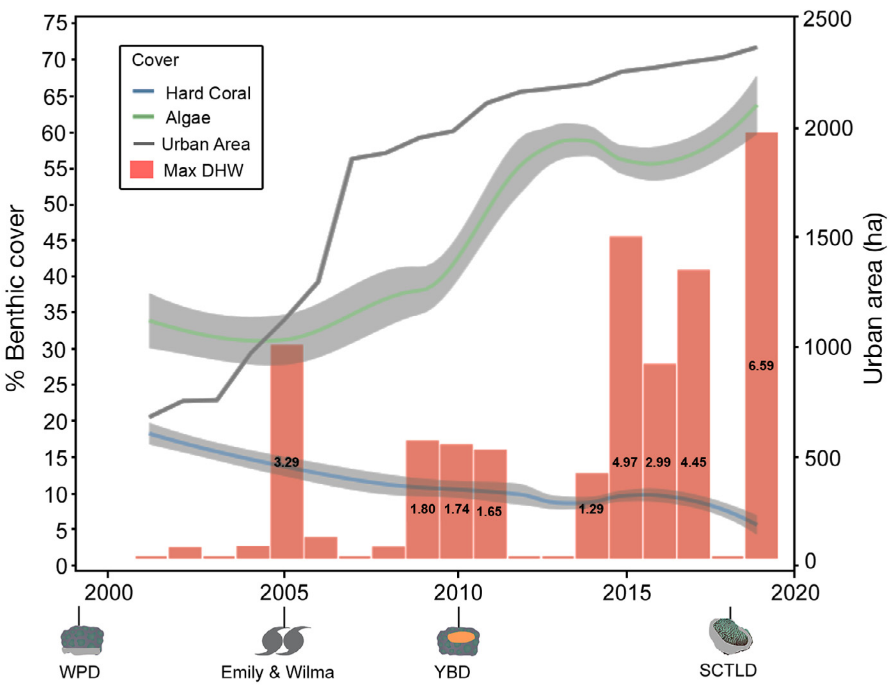

Fig. 7. Benthic cover changes and stressors timeline between 2001 and 2019 in Akumal Reef. Coral cover is represented by a blue line, total algae cover by a green line, urban area by a grey line, and maximum degree heating weeks (Max DHW) by orange bars. The shading represents the 95% confidence interval for the coral and algae cover curve. Years impacted by hurricanes and disease outbreaks are noted on the x-axis. WP: white plague; YBD: yellow band disease; SCTLD: stony coral tissue loss disease; Emily & Wilma: hurricane names. Adapted from Randazzo-Eisemann et al. (2021b)

reef-based tourism, as its main attractions are unparalleled access to sea turtles, sandy beaches, and coral reefs (Gil et al. 2015). Tourist services in Akumal account for 10% of employment in the Riviera Maya, being the principal source of income for Tulum Municipality, and approximately 80% of the Akumal population work directly in tourism services (Mata-Lara et al. 2018). Yet, former studies in Akumal emphasize that interactions between multiple stressors, such as urban area along with precipitation and nitrogen-rich waters along with thermal stress, have eroded coral reef resilience, increasing the system's vulnerability to mass bleaching and disease outbreaks (Randazzo-Eisemann et al. 2021b). Thus, the long-term persistence of sustainable tourism services in Akumal may depend to a degree on the recovery of both coral cover and the diversity of its coral assemblages. These goals must be addressed through urgent management actions applied at multiple scales.

Firstly, in addition to the current management tools implemented in the area — such as the Akumal Fishing Refuge (DOF 2015), the Reserve for Aquatic Species Protection (DOF 2016a), and the Mexican Caribbean Biosphere Reserve (DOF 2016b) — integrative management strategies are required to improve conditions favorable to coral and not macroalgae. For instance, it is important to implement additional wastewater management strategies to diminish local chronic stressors (Souter et al. 2021) linked to urban/tourism development, as the Yucatan karstic landscape is highly affected by land-based pollutants, such as nutrients, the concentrations of which have been high in the last decade (Hernández-Terrones et al. 2011, Naranjo-García 2016). Such actions will be vital to give Akumal Reef a better chance to face stochastic events such as disease outbreaks, as well as coral bleaching and associated mortality events, which are predicted to become more frequent and intense (Januchowski-Hartley et al. 2017).

Secondly, due to the lack of recruitment of structurally complex coral species, active restoration might be a powerful tool to target the restoration of diverse coral assemblages. Currently, a restoration project led by 'Centro Ecológico de Akumal' and the Akumal community is being implemented on Akumal Reef, with a strong participation component and a focus on finding long-term sustainable strategies. We suggest that to potentially enhance Akumal reef physical functionality, the restoration efforts carried out by the project should include the genera *Acropora*, *Colpophyllia*, *Dendrogyra*, *Orbicella*, *Diploria*, and *Pseudodiploria*, which have higher calcification rates, higher rugosity, and larger sizes.

Presently, the global challenge is to steer reefs through the Anthropocene in a way that maintains their biological functions (Hughes et al. 2017), and one way to accomplish this challenge is to scale up from local to global levels, implementing local solutions to global problems. We recommend the implementation of simultaneous multiple-scale management actions that integrate both coastal planning and active restoration of structurally complex coral species. Addressing the multiple causes of the lack of recovery of critical reef functions in Akumal might give a window of opportunity to maintain its future capacity to provide habitat and environmental services.

5. CONCLUSIONS

The significant loss in coral cover, particularly of stress-tolerant coral species from 2001 to 2019, resulted in all reef sites currently being dominated by small, non-framework building weedy coral species, with most of these sites having coral cover <10%. These 2 signs of reef decline — weedy species dominance and low coral cover — were possibly driven by the cumulative effects of increased stressors and algae, and together they lead to reef physical functionality loss, and the overall homogenization of functional coral traits. To maintain Akumal Reef's critical functions and vital services to sustaining Akumal's coastal communities (such as coastal protection and tourism), it is essential and urgent to focus on multi-scale management strategies that can significantly diminish local chronic stressors linked to urban/tourism development and actively restore framework-building coral species.

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