

Fine-scale thermal stress heterogeneity decouples bleaching from mortality across a Caribbean fringing reef

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Abstract

Marine heatwaves are becoming more severe, yet reef outcomes vary dramatically at local scales. We document the biological consequences of the 2023 marine heatwave, the most intense on record, across the Puerto Morelos fringing reef, Mexico, where 13 sites within 40 km experienced nearly twofold variation in accumulated thermal stress. Repeated surveys across increasing-stress, peak-stress, and post-bleaching periods, combined with long-term benthic monitoring (1985–2024), show that bleaching was near-universal across taxa and sites. Yet, mortality was strongly decoupled from bleaching prevalence, varying markedly by taxon and local thermal stress. Bleaching probability increased with DHW for all genera, but acute mortality was concentrated in heat-sensitive taxa (*Acropora* and *Millepora*), whereas thermally tolerant reef-builders bleached extensively but largely recovered at sites with the lowest stress levels. Site-level community trajectories revealed divergent post-bleaching outcomes across local DHW conditions, with the most thermally stressed sites showing increasing colony mortality, whereas low-stress sites showed signs of recovery, even where communities were dominated by susceptible species. This thermal gradient was consistent with reported differential wave-driven water exchange modulated by the Yucatán Current, rather than species composition or depth. Against a backdrop of decades-long decline, live coral cover and reef physical functioning fell to critically low levels, reflecting the compounding impacts of the marine heatwave and previous outbreaks of Stony Coral Tissue Loss Disease. Our findings demonstrate that fine-scale oceanographic heterogeneity determines reef fate during marine heatwaves and identify thermally sheltered sites as priorities for monitoring and genotypically informed restoration.

Introduction

Coral reefs are increasingly susceptible to anthropogenic climate change, particularly marine heatwaves, which are becoming more frequent, longer, and intense as greenhouse gas emissions continue (Frölicher et al., 2018; Oliver et al., 2019). Marine heatwaves are periods of unusually warm water that can drastically affect coral communities when they persist above temperature thresholds (Hughes et al., 2018b; Starko et al., 2024). The increasing duration and intensity of these events have driven higher frequency and severity of coral bleaching and associated mortality worldwide (Hughes et al., 2018b; Bove et al., 2022). Bleaching signals physiological stress and can produce a range of sublethal effects, including reduced growth and reproduction, but prolonged or extreme warming overwhelms the physiological capacity of reef corals to tolerate stress, leading to death (Carballo-Bolaños et al., 2020). Consequently, bleaching events are becoming more pronounced globally, resulting in widespread mortality due to cumulative heat stress (Skirving et al., 2019; Hughes et al., 2018b; van Woesik et al., 2022; Eakin et al., 2026).

February 2023 marked the onset of what is now recognised as the most intense and extensive global coral bleaching event on record (Spady et al., 2026; Hoegh-Guldberg et al., 2023). Satellite-based analyses by the U.S. National Oceanic and Atmospheric Administration indicate that between 2023 and 2024, more than 80% of the world's coral reef areas experienced bleaching-level heat stress (NOAA,

2024). The severity of bleaching and resulting mortality is determined by both the magnitude and duration of thermal stress, typically quantified by the Degree Heating Week (DHW; °C-week) metric, which integrates excess temperature over time (Liu et al., 2014; Donner et al., 2017). This episode was exceptionally severe in the Atlantic, where nearly all reefs recorded bleaching-level heat stress. In many regions, heat stress began roughly two months earlier than in previous events, producing prolonged anomalously high temperatures that far exceeded normal seasonal variability. Consequently, DHW values reached levels 2–3 times greater than any previously observed in the satellite record (Reimer et al., 2024).

Even under the same extreme thermal stress, coral species respond differently (Chollett et al., 2014; Shlesinger et al., 2023). These species-specific responses arise from differences in holobiont biology (host physiology, algal symbionts, and microbiome) and from interactions with other organisms (Voolstra et al., 2021; Marangon et al., 2025). Consequently, coral communities follow complex post-disturbance trajectories driven by species-specific heat tolerance and shifts in relative abundances (Loya et al., 2001; Bove et al., 2019; Mydlarz et al., 2010; Hoadley et al., 2015). In the Caribbean, taxa such as *Agaricia* spp. and branching *Porites* spp. show early bleaching and high peak mortality, whereas massive corals, although susceptible, often experience sublethal impacts rather than widespread whole-colony mortality (Smith et al., 2013; Muñiz-Castillo et al., 2024). Evidence for *Acropora* spp., the region's main reef-builders, is noteworthy. The genus is generally regarded as thermally sensitive (Marzonie et al., 2023; Randall and Szmant, 2009), yet *Acropora palmata* has exhibited unexpected resilience during previous bleaching events (Kuffner et al., 2020; Muñiz-Castillo et al., 2024; Williams et al., 2017). During the 2023–2024 event, however, *A. palmata* populations experienced severe declines and appear to have nearly disappeared from many shallow reefs across the region (Miller et al., 2024; Williams et al., 2024; Manzello et al., 2025; Birkart & Alvarez-Filip, 2025).

Moreover, local-scale environmental variability strongly modifies coral thermal tolerance beyond species-level susceptibility or individual acclimatization (e.g., Cuning et al., 2021). Local-scale drivers such as reef geomorphology, hydrodynamics, and depth gradients, also create spatially heterogeneous temperature regimes over tens to hundreds of meters (Pineda et al., 2013; Zhang et al., 2013; Penin et al., 2007; Grimsditch et al., 2010; Green et al., 2019; Pérez-Rosales et al., 2026). These processes alter residence time and the exchange of reef water masses, producing conditions in which corals experience markedly different peak temperatures and variability from those at adjacent sites (Safaie et al., 2018; Meoded-Stern et al., 2025). Because most satellite-based products average temperature at coarse (~ 1 to 5 km) resolution and integrate sea-surface signals, they can predict similar bleaching-level stress for neighboring reefs while missing critical local-scale heterogeneity that drives contrasting thermal exposure and bleaching outcomes (Bos & Pinsky, 2025; Liu et al., 2024; Sakai et al., 2019). High-resolution hydrodynamics reveal patterns such as enhanced variability that can increase coral acclimatisation potential, or conversely, prolonged residence of warm water that elevates mortality risk (Brown et al., 2023; Voolstra et al., 2021). Ultimately, under increasingly thermally stressful conditions, understanding fine-scale thermal variability will be crucial for implementing meaningful management strategies at operational scales (Grimaldi et al. 2023).

Ultimately, the post-disturbance trajectories of coral communities determine future ecological dynamics and ecosystem functionality on affected reefs (Hughes et al., 2018b; Zinke et al., 2018). To depict potential pathways followed by species or sites during and after severe marine heatwaves, we developed a conceptual framework in which individual coral colonies occupy one of three states at a given reef: healthy, stressed (pale or bleach present), or dead (complete colony mortality; Fig. 1). Species-specific susceptibility and the magnitude and duration of thermal stress together set the fraction of colonies that transition from healthy to stressed, and the fraction of stressed colonies that progress to mortality, a process that can be deferred, with physiological exhaustion and post-stress mortality occurring weeks to months after peak temperatures (Jones, 2008; Baker et al., 2008; Voolstra et al., 2025; Fig. 1). Applying this framework, we quantified species-level susceptibility across a semi-continuous series of fringing reefs that experienced varying heat exposure during the 2023 event. We demonstrate that although most species exhibited bleaching, net losses depended on both inherent species susceptibility and the local magnitude of heat stress experienced by each reef. Finally, we contextualize the ecological and functional consequences of the 2023 marine heatwave using a longer-term time series from the same reefs to evaluate persistence, recovery potential, and trajectory of reef degradation.

Methods

Study area

We assessed impacts of the 2023 bleaching event at 13 sites (10 back-reef, 3 fore-reef) in Puerto Morelos, Quintana Roo, México (Fig. 2). This fringing reef system stretches 1–3 km parallel to the coast in a semi-continuous formation with distinct back-reef, reef-crest, and fore-reef zones influenced by wave exposure and light. Reefs within this system have undergone ecological homogenization over the past 31 years, driven largely by declines in framework-building branching *Acropora* spp. and foliose–digitiform corals in the back-reef and relative increases in non-framework species (*Agaricia agaricites*, *Porites astreoides*) on the fore-reef (Estrada-Saldívar et al., 2019). Nonetheless, some sites in Puerto Morelos retained abundant *A. palmata* populations prior to the 2023 heatwave event (Birkart et al., 2025; de Hoyos-Jiménez et al., 2025; Rodríguez-Martínez et al., 2014)

Site surveys

All surveys followed Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocols (Lang et al., 2012). At each site, coral assemblages were sampled with 10 × 1 m belt transects placed haphazardly within the same depth and reef zone. To examine temporal change associated with the heatwave event, we defined three survey periods: increasing stress conditions (July 2023; 8 sites and 27 transects), peak heat stress (August–October 2023; 13 sites, 76 transects; note two sites were surveyed more than once during this period), and post-bleaching (November 2023–March 2024; 9 sites, 57 transects). For every live coral colony encountered in each transect, we recorded species, colony dimensions (maximum diameter, perpendicular diameter, and height), percent bleaching, percent partial mortality (new, transition, old),

presence of disease, and completely recent mortality attributable to bleaching. We also recorded colonies with 100% recent mortality attributable to bleaching (Table S1). Here, coral species were classified based on their physiological susceptibility to thermal stress: vulnerable or heat-sensitive taxa (*Acropora* sp., *Agaricia* sp., and *Millepora* sp.), thermally tolerant reef-builders (e.g., *Orbicella* sp. and *Pseudodiploria* sp.), and thermally tolerant weedy species (e.g., *Porites*).

Long-term change in the ecological and functional structure of coral communities

To place short-term responses in a longer-term context. We first used benthic cover data from eight sites for the years 2016 and 2020–2024 (Fig. 2), collected using AGRRA benthic methods: six 10 m transects per site, placed haphazardly and parallel to shore, with point-intercept sampling at fixed intervals and transects spaced 5–25 m apart. Second, we also incorporated historical benthic data from this reef system (1985; Estrada-Saldívar et al., 2019) to contextualize trends in coral cover and community change. Lastly, using all available information, we quantify species-specific contributions to reef structure and function through time. We then calculated the Reef Functional Index (RFI; González-Barrios & Álvarez-Filip, 2018), which ranges from 0 to 1, with values approaching 1 indicating dominance by species with high structural complexity and calcification rates, and thus greater reef functionality. Similar to the above, coral taxa were grouped by life-history strategies and ecological functionality: *Acropora* sp., *Orbicella* sp., massive, and weedy species (González-Barrios et al., 2021), but we also included one group based on their high vulnerability to the 2023 bleaching event: vulnerable or heat sensitive (*Millepora* sp. and *Agaricia* sp.).

Heat stress data

In situ temperature data (60-min intervals) were obtained from different reef sites using two complementary sources. We deployed temperature loggers at two sites between January 2023 and March 2024. Additionally, data from loggers deployed by NGO partners were incorporated for five sites monitored from September 2022 to August 2023. For each data logger, we computed daily mean temperature from nighttime measurements to minimise diurnal surface heating bias; daily means were then averaged by site within each month to produce monthly mean daily temperature and monthly temperature range. These *in situ* time series were used to classify the two survey periods described above.

For the same sites, satellite sea-surface temperature (SST) and NOAA Coral Reef Watch (CRW) Degree Heating Weeks (DHW) products were retrieved (NOAA, 2024). We then calculated DHW from the *in situ* record using CRW-derived climatology parameters. Specifically, CRW climatology (1985–2024) and the maximum monthly mean (MMM; the warmest monthly mean over the climatology) were obtained from CRW for each site. The bleaching threshold was set as $MMM + 1.0^{\circ}\text{C}$ and applied to the *in situ* temperatures. Heat accumulation (DHW) was computed using a 12-week (84-day) sliding window: for

each day, positive temperature anomalies (daily mean – bleaching threshold, when > 0) were summed over the preceding 84 days and expressed in °C-weeks (sum of daily anomalies divided by 7). The sliding window advanced one day at a time to produce a continuous DHW time series comparable to the CRW product.

To evaluate the relationship between thermal stress and coral bleaching, we modelled the proportion of stressed (i.e., visibly pale or bleached) colonies as a function of accumulated heat stress (DHW) and coral genus. Bleaching responses were analysed using a generalised linear mixed-effects model (GLMM) with a binomial error distribution and logit link, specifying the response as the number of stressed versus non-stressed colonies (`cbind(Stressed, Total-Stressed)`). Fixed effects included DHW, genus, and their interaction to assess both the overall effect of thermal stress and genus-specific differences in response. Site was included as a random intercept to account for spatial variation. To ensure model stability and avoid issues related to low sample sizes and separation, analyses were restricted to genera with sufficient representation (≥ 5 observations and ≥ 30 total colonies). Genus-specific responses to DHW were quantified by estimating marginal trends (`emmeans`), providing effect sizes and confidence intervals for each taxon. Then, to evaluate the relationship between thermal stress and coral mortality, we modelled the proportion of dead colonies as a function of accumulated heat stress (DHW) and coral genus using a generalised linear mixed-effects model (GLMM) with a binomial error distribution (`cbind(Dead, Total - Dead)`). Fixed effects included DHW, genus, and their interaction, with site as a random intercept. Analyses were restricted to genera with sufficient representation (≥ 5 observations and ≥ 30 colonies). Genus-specific responses were estimated using marginal trends (`emmeans`).

Pathways of change after the heatwave event

To explore the responses of different coral taxa to increasing heat stress, we first calculated the percentages of colonies observed as stressed or dead during the peak stress period. Post-stress percentages were calculated by aggregating observations (one survey per site) from the post-stress survey window (November 2023–March 2024). Post-stress bar plots show site-pooled percentages per genus. Genera were plotted only when sample size per species across sites exceeded a minimum threshold (> 30 colonies and > 3 sites) to ensure robust curve fits; rare taxa were omitted. Analyses and figures were produced in R.

Then, to represent the pathway of coral community states (proportions of healthy, stressed/bleached, and recently dead) across sites and survey periods (peak and post-stress), we calculated the proportions of colonies in three categories: healthy, stressed/bleached, and recently dead, using colony-level records from surveys. We then transformed the three proportions into ternary coordinates and plotted site points on ternary diagrams. Data processing and plots were produced in R (data wrangling with `dplyr`; ternary plotting with `ggtern` or `ggplot2` extensions).

Results

Thermal stress depends on local oceanographic conditions

Despite the proximity of the sites (~ 40 km apart), we found substantial variability in accumulated thermal stress (DHW) across the study area. Northern sites (Limonas, Manchones) experienced the lowest stress (13–15 maxDHW) yet still indicated a considerable level of thermal accumulation and bleaching risk. The mid–southern and southern sites (Jardines, La Pared, Punta Maroma) registered extreme levels of stress (17–19 maxDHW), consistent with substantial bleaching and a high probability of multiple-species mortality. The greatest heat accumulation occurred at several central sites (21–24 maxDHW), indicating prolonged, severe thermal exposure associated with a high probability of multiple-species mortality. The observed spatial pattern suggests that local dynamics, such as oceanography or reef morphology, play a significant role in modulating coral reef responses to disturbances.

Impacts of coral communities

During the heatwave (increasing stress window), the probability of colonies exhibiting bleaching increased with accumulated DHW for all taxa (GLMM, $\beta = 0.34 \pm 0.05$, $p < 0.001$; Fig. 3b; Table S2 and S3). This relationship was consistent but varied in magnitude among genera, as indicated by a significant DHW $\times$ Genus interaction, with all analysed taxa showing positive responses to increasing thermal stress. Genera such as *Orbicella*, *Agaricia*, and *Porites* showed the highest proportions of stressed colonies even at moderate DHW, reaching above 80% of all colonies at the highest levels of stress. Genus-specific slopes ranged from lower responses in *Millepora* ($\beta \approx 0.20$) to stronger responses in *Porites* and *Pseudodiploria* ($\beta \approx 0.46$ – 0.49), highlighting differential sensitivity to thermal stress. In contrast, mortality accumulation during peak stress (Fig. 3c) increased with accumulated DHW (GLMM, $\beta = 0.48 \pm 0.11$, $p < 0.001$, Table S4) and was primarily driven by a subset of genera, as indicated by genus-specific DHW slopes (Table S5): *Acropora* and *Millepora* showed the largest increases in mortality rate with rising DHW, with additional but comparatively weaker increases detected in *Porites* and *Agaricia*, whereas massive taxa (e.g., *Orbicella*, *Siderastrea*, *Pseudodiploria*) exhibited minimal mortality until very high DHW. The post-stress evidence (Fig. 3d,e) indicates that while many species had a substantial proportion of stressed colonies, the largest net losses (percent dead; Fig. 3e) were concentrated in *Acropora*, *Millepora*, and *Agaricia*. Interestingly, this last genus showed a clear transition from stressed to dead during a period when stress conditions were declining, suggesting physiological exhaustion leading to post-stress mortality, in contrast to the mortality observed in *Acropora* and *Millepora*, which largely occurred during the period of stress accumulation. Overall, there is a decoupling between bleaching prevalence and mortality risk, underscored by species-specific vulnerability thresholds and potential for legacy mortality after peak temperatures subside.

Pathways of change after the heatwave event

We examined coral-community trajectories at peak and post-peak phases of the 2023 heatwave using ternary plots grouped by functional/thermal categories: (1) vulnerable or heat-sensitive framework taxa

(*Acropora*, *Millepora*, *Agaricia*), (2) thermally tolerant reef-building taxa (e.g., *Orbicella*, other massive species), and (3) thermally tolerant weedy taxa (small, fast-growing species) (Fig. 4). At peak stress, all groups shifted toward higher proportions of stressed (bleached) colonies, but responses diverged thereafter. Heat-sensitive taxa showed the greatest increase in mortality, with some sites experiencing > 50% recent mortality. Thermally tolerant reef-builders became heavily bleached but largely avoided widespread mortality, with many sites moving back toward the healthy/stressed boundary in the post-stress window, indicative of recovery. Weedy taxa bleached broadly and exhibited intermediate mortality: higher than reef-builders but generally below catastrophic levels ($\leq 50\%$) at most sites (e.g., Tanchacte Sur, Tanchacte Norte, and Bonanza).

Furthermore, trajectories were strongly site-dependent and correlated with local maxDHW. Lower-stress sites (e.g., Limones, Manchones; ~ 15 DHW) reverted toward healthier states post-peak, whereas high-stress sites (e.g., La Bocana, Rodman, La Catedral, Radio Pirata; 26–27 DHW) continued toward an increased proportion of dead colonies, reflecting stress-legacy mortality. Sites with lower measured thermal exposure showed the smallest compositional shifts overall, remaining closer to the healthy-stressed sector of the ternary plots. These patterns demonstrate that post-heatwave outcomes reflect an interaction between species-level heat susceptibility and local heat exposure: thermally tolerant reef-builders exhibited the greatest capacity to recover with low mortality, while vulnerable species suffered the largest net losses, and weedy taxa occupied an intermediate position in mortality risk. Overall, these results indicate that coral community responses to extreme thermal events depend on both species-specific susceptibilities to heat stress and reef-building capacity. Thermally tolerant reef-building corals showed the highest resilience, recovering from bleaching with low mortality, while thermally tolerant weedy corals exhibited slightly higher mortality levels.

Long-term trajectory of change on coral cover and reef functionality

Longer-term analyses of time series from the same reefs show that total live coral cover has declined markedly from the historical baseline to the present (Fig. 5). Mean cover fell from $\sim 35\%$ in 1985 to $\sim 20\%$ by 2016–2020 and continued to decline through 2024 to roughly 8–10%. Reef physical functionality (depicted by RFI) followed a similar downward trajectory, with a steep decline after the 2023 heat stress event, largely due to a progressive loss of reef-building and structurally important taxa, as well as overall functional capacity. Taxon-level changes underlie these trends. *Acropora* dominated historical cover in 1985 but collapsed by 2016 and remained at very low abundances thereafter. During 2023, acroporids experienced severe relative losses, although this appears to be a negligible decline when compared to the historical cover of this genus. The decline of acroporids largely accounted for the drastic reduction in RFI observed in 2024. *Orbicella* and other massive species contributed modestly over the years and experienced moderate, albeit more gradual, losses. However, by 2024, massive species became a relatively large portion of coral communities, owing to their higher levels of thermal tolerance (Fig. 3). In contrast, vulnerable taxa (*Agaricia* and *Millepora*) increased in relative representation after 1985 and

accounted for a larger fraction of the reduced total cover by 2016–2024; however, they underwent severe losses during the 2023 heatwave. In contrast, weedy corals (largely dominated by *Porites astreoides*) have consistently increased in relative representation over time. Overall, the combined effect is a marked shift from a high-cover, structurally complex reef community toward lower total cover, with proportionally greater representation of smaller, lower-framework taxa, resulting in the observed decline in RFI and suggesting reduced capacity for structural complexity and reef accretion.

Discussion

The 2023 marine heatwave was the most severe bleaching event on record (Spady et al., 2026; Hoegh-Guldberg et al., 2023), and the Puerto Morelos fringing reef system was no exception to its deadly consequences. Yet our results reveal a striking degree of heterogeneity in outcomes across a reef system spanning less than 40 km. Accumulated heat stress varied nearly twofold among sites, ranging from 13 maxDHW at northern sites to 25 maxDHW at central locations, a gradient attributable to local oceanographic processes governing water exchange and thermal residence time rather than to differences in species assemblages or depth (Safaie et al., 2018; Green et al., 2019; Grimaldi et al., 2023; Meoded-Stern et al., 2025). This fine-scale thermal variability had profound biological consequences. Although bleaching was ubiquitous across taxa and sites, underscoring the severity of the heatwave, mortality was strongly decoupled from bleaching prevalence and varied markedly by taxon and locally experienced thermal stress. Vulnerable species (*Acropora*, *Millepora*) suffered acute mortality during stress accumulation (see also Birkart & Alvarez-Filip, 2025); *Agaricia* exhibited delayed post-stress mortality consistent with physiological exhaustion (Jones, 2008; Baker et al., 2008); and thermally tolerant reef-builders (*Orbicella* and other massive corals) bleached extensively but largely recovered, particularly at lower-stress sites. The interaction between inherent taxon susceptibility and locally experienced DHW determined whether reefs followed a trajectory of recovery or progressive collapse. These dynamics unfolded against a backdrop of decades-long functional decline (Estrada-Saldívar et al., 2019).

Our results reveal a strong decoupling between bleaching extent and subsequent mortality across coral taxa and nearby reef sites, suggesting that bleaching prevalence alone may be a poor predictor of demographic impacts during marine heatwaves. Although bleaching became nearly universal across taxa and sites, mortality remained strongly species- and site-dependent even across distances of hundreds of meters, which is consistent with the established finding that bleaching susceptibility does not predict subsequent mortality across taxa (Grottoli et al., 2006; Hughes et al., 2018b; Matsuda et al., 2020; Yadav et al., 2023). *Acropora* and *Millepora* experienced rapid mortality during thermal stress accumulation, reflecting the vulnerability of branching taxa with thin tissues and limited energetic reserves (Loya et al., 2001). For *Acropora*, it has been shown that the species exhibits only ~ 1°C seasonal variation in its photochemical thermal threshold compared to ~ 3°C in more physiologically flexible taxa, constraining its capacity to shift its tolerance ceiling before a sudden extreme event (García et al., 2024). Whereas genera such as *Agaricia* showed delayed mortality weeks after peak temperatures, consistent with temporary heterotrophic buffering during bleaching, which can delay the onset of mass

mortality, followed by progressive energy exhaustion once lipid stores fall below the critical survival threshold (Rodrigues & Grottoli, 2007; Anthony et al., 2009). Differences in the timing and severity of mortality among taxa may also reflect distinct physiological and cellular responses to thermal stress, as molecular studies have documented rapid apoptotic processes (programmed cell death) in zooxanthellate corals exposed to elevated temperatures (Tchernov et al., 2011). While the ‘winners and losers’ framework proposed by Loya et al. (2001), based on differences in colony morphology and tissue thickness, explains important variation in species susceptibility to thermal stress, our results further suggest that these trait-mediated responses are strongly modulated by how the marine heatwave manifested locally in terms of the thermal stress actually experienced by organisms, allowing substantially different ecological outcomes even across nearby reef sites (van Woesik & Randall, 2017; Safaie et al., 2018; Palumbi et al., 2014).

Superimposed on this physiological hierarchy, locally experienced thermal dose determined whether species-specific thresholds were crossed at each site. The strong contrast between satellite-derived and in situ estimates of accumulated heat stress suggests that neighbouring reefs did not experience the 2023 thermal anomaly uniformly. Although NOAA products estimated approximately between 14 and 15.13 DHW across the four pixels (Liu et al., 2024) encompassing all study sites, local temperature records revealed substantially different levels of accumulated thermal stress among reefs located only a few kilometres apart. At lower-DHW sites (e.g., Limones, Manchones), some sensitive taxa partially recovered, whereas at higher-DHW sites (e.g., Tanchacte) even typically tolerant corals remained stressed or bleached, indicating that sufficiently severe thermal stress can override conventional tolerance patterns. At Puerto Morelos, the DHW gradient along the reef is likely generated by differential wave-driven water exchange including surface wave breaking over the reef crest, which drives 87% of lagoonal transport variability, with water turnover times ranging from approximately two hours under normal Trade Wind swell to several weeks during extended summer calms (Coronado et al., 2007). Northern sites flush more efficiently; central and southern sites accumulate heat as wave energy drops and as seasonal intensification of the Yucatán Current lowers coastal sea level through geostrophic balance, further reducing wave overtopping efficiency precisely when temperatures peak (Coronado et al., 2007; Torres-Freyermuth et al., 2012). Analogous patterns have been reported elsewhere where wave-exposed sites bleached substantially less compared to sheltered site in Colombia despite no regional temperature difference (Bayraktarov et al., 2013), and sheltered subtropical sites bleached more severely than wave-exposed sites in Hong Kong under the same regional heat stress (Chung et al., 2024). The full spectrum of 2023 outcomes across Puerto Morelos therefore reflects the interaction of taxon identity and local oceanography; neither alone is sufficient to predict reef fate at the spatial scales that matter for management (Starko et al., 2024).

The fourth global coral bleaching event represents a critical tipping point within a trajectory of coral decline spanning four decades across the Caribbean. Since the 1970s, Caribbean reefs have sustained near-continuous losses, with hard coral cover declining by roughly 80% across the region (Wicquart et al., 2025). At Puerto Morelos, the local trajectory mirrors this regional pattern with live coral cover falling from ~ 35% in 1985 to barely ~ 8% by 2024 (Estrada-Saldívar et al., 2019; Fig. 5). Critically, however,

functional loss has outpaced cover loss, with the Reef Functional Index reaching critically low levels after 2023, reflecting the sequential erosion of successive morpho-functional groups through two distinct disturbance events. The first was the outbreak of Stony Coral Tissue Loss Disease (SCTLD), which at our study sites disproportionately targeted reef-building massive species, stripping assemblages of their primary carbonate-producing component and driving marked reductions in reef structural complexity and accretion potential (Estrada-Saldívar et al., 2020; Alvarez-Filip et al., 2022). Across the wider Caribbean, SCTLD alone caused a decline in reef accretion potential of more than 70% within six years at affected sites, reducing mean accretion rates to near zero and pushing reefs into effective accretionary stasis (Toth et al., 2023). The second was the 2023 heatwave, which decimated populations of *Acropora palmata* and other heat-sensitive taxa that had largely escaped SCTLD, delivering a compounding blow to the functional groups on which reef structural complexity most depends (Birkart & Alvarez-Filip, 2025; Manzello et al., 2025). The particular consequences of this loss extend beyond coral cover, as branching taxa such as *Acropora* contribute disproportionately to reef framework development but may also undergo particularly rapid structural collapse following mortality, fragmenting into mobile rubble that can accelerate declines in both reef three-dimensional complexity and vertical accretion compared to the more gradual erosion typical of massive morphologies (Molina-Hernández et al., 2022; Morais et al., 2022). Each of these events stripped a different functional layer, leaving communities increasingly dominated by thermally tolerant massive and weedy taxa, not because these species are thriving, but because everything structurally important has declined more steeply, producing assemblages with markedly reduced capacity for vertical accretion and habitat provision (Lange & Perry, 2019; González-Barrios et al., 2021). This sequential erosion of functional groups unfolds against a backdrop of rapidly shrinking recovery windows (Hughes et al., 2018a), and empirical analyses spanning a 36-year time series show that full recovery to historical benchmarks occurred in only a fraction of disturbance events (Emslie et al., 2024). The structural consequences of this compounding pattern are legible in reef carbonate budgets at the regional scale. Even before SCTLD and the 2023 heatwave, approximately 37% of Caribbean reef sites were already net erosional, with carbonate production at least 50% below Holocene averages (Molina-Hernández et al., 2020; Perry et al., 2013), and the combined effects of disease and bleaching have now pushed these trends past a critical threshold, with over 70% of Caribbean reef sites having shifted into net erosional states (Álvarez-Filip et al., 2026). This represents a fundamental transition not merely in coral cover, but in the physical architecture of reefs and their capacity for vertical accretion, habitat provision, and coastal protection.

Our findings have immediate implications for reef monitoring and management under increasing thermal stress. First, it highlights the importance of spatially replicated, long-term ecological monitoring as an irreplaceable conservation tool. The patterns documented here are only visible because standardised surveys were maintained consistently across sites and years. Importantly, our findings also highlight the importance of resolving key physicochemical conditions underlying bleaching responses at ecologically relevant spatial scales. Although satellite-derived thermal products remain invaluable for early warning systems and broad-scale assessments, they may fail to capture the fine-scale thermal heterogeneity experienced by shallow coral reefs, potentially obscuring local thermal environments that ultimately

shape bleaching outcomes. Yet in Mexico and other nations there has been a marked institutional shift over the last decade toward directing resources away from ecological monitoring and toward active interventions such as coral restoration, with the 2023 event itself generating insufficient funding and interest for systematic impact assessment. This reallocation is counterproductive, as without knowing where thermal refugia exist, which functional groups are declining, and which sites retain recovery potential, restoration efforts cannot be prioritised rationally, and their outcomes cannot be evaluated against a meaningful baseline (e.g., Muñoz-Castillo et al., 2024). We therefore urge local and international governmental agencies and organisations interested in reef conservation to recognise the value of monitoring and consider restoration and other interventions as a complement rather than a replacement in the management tool of coral reefs; otherwise, decisions such as what sites to protect or which coral would be a source of resistant genotypes will be based on conceptual ideas rather than clear and informed evidence. Likewise, the long-term monitoring of restoration interventions is the only manner we will be able to understand how our interventions are driving reef recovery (Boström-Einarsson et al. 2020), which is particularly important given that wild and restored populations will be subject to the same level of stress under increasing climatic pressures.

We found that sites experiencing the lowest thermal stress, particularly the northern sites of Limones and Manchones, retained the highest coral cover, showed the greatest recovery capacity among thermally tolerant taxa, and represent the most viable targets for protection. These sites act as thermal refugia, locations that escape peak thermal exposure through local oceanographic conditions rather than through biological resistance (McClanahan et al. 2023), and constitute rational priorities for local stressors reduction, restricted access, and donor-coral sourcing for restoration at more thermally exposed locations (Meoded-Stern et al., 2025; Birkart et al., 2025; Melo-Merino et al., 2026). However, they are not permanent refugia, as survival may reflect milder exposure rather than heat-tolerant genotypes, and both acclimatisation and genetic adaptation influence tolerance (Palumbi et al., 2014; Drury, 2020; Carballo-Bolaños et al., 2020). Consequently, genotypic screening should accompany any propagation or restoration to avoid spreading heat-sensitive survivors as resilient corals (Cunning et al., 2021; Miller et al., 2024). Moreover, the thermal shelter these sites currently provide is finite and contingent on continued global warming trajectories: the fraction of global reef pixels functioning as local-scale thermal refugia is projected to fall dramatically as global warming increases (Dixon et al., 2022). Ultimately, local and regional interventions can buffer outcomes at the margin but cannot counteract the trajectory set by continued greenhouse gas emissions: at the highest-stress sites documented here, the question is no longer where to focus restoration efforts, but whether sufficient live coral and suitable substrate will remain to make those efforts viable at all (Manzello et al., 2025; Birkart & Alvarez-Filip, 2025; Emslie et al., 2024).

The scale and pace of change documented here leave little room for complacency about the near-term trajectory of Caribbean coral reefs in the absence of decisive action at the global scale. The 2023 event was unprecedented in its severity and geographic extent (Spady et al., 2026; Hoegh-Guldberg et al., 2023). These levels of stress are, however, predicted to become more prevalent under current scenarios; climate change is likely to intensify, with some models projecting near-annual bleaching on most reefs

within decades (Frölicher et al., 2018; Mellin et al., 2024; Zeng et al., 2025). Avoiding the worst outcomes will require, above all, rapid and sustained reductions in greenhouse gas emissions to slow the rate of ocean warming and preserve the recovery windows that allow even the most vulnerable reef systems some prospect of persistence. In parallel, protecting oceanographically sheltered sites from local stressors, sustaining long-term ecological monitoring, and implementing genotypically informed restoration represent the most viable near-term strategies for maintaining some reef functionality in the Caribbean, but these actions will be effective only as a complement to, not a substitute for, the global emissions response that reef systems most urgently demand.

Declarations

Conflict of interest

The authors declare no competing interests.

Author Contribution

Conceptualisation by all other authors, fieldwork by all other authors, data analysis by L.A-F, A.M-H., N.E-S. Data systematisation and integration by E.P-C. Manuscript writing was performed by L.A-F, A.M-H, N.E-S. All authors revised and approved the manuscript.

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Data Availability

The data that support the findings of this study are available within the paper and in the Supplementary Information. Any additional data not found within are available from the authors upon request.

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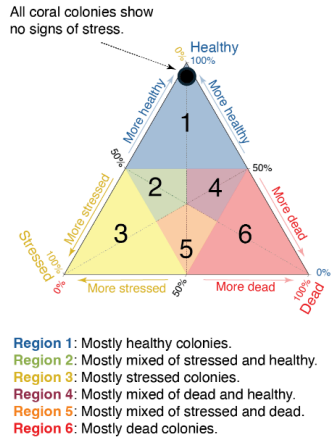
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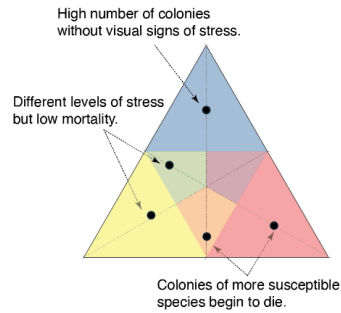
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Figures

a) Non-thermally stressful conditions



b) Peak-stress conditions



c) Post-stress conditions

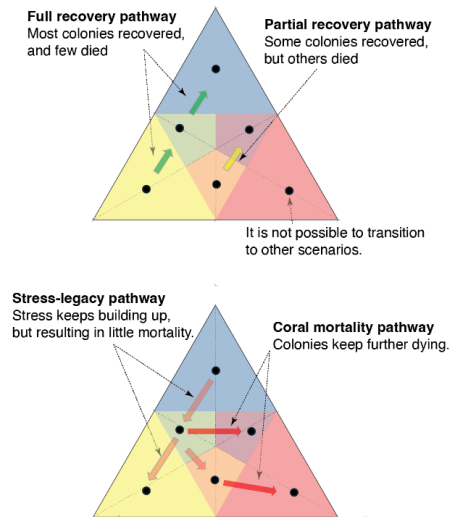


Figure 1

Conceptual diagram of coral-community trajectories before, during, and after a marine heatwave. Each ternary plot depicts the ratios of healthy (top vertex), stressed (left), and dead (right) colonies. (a) Pre-stress: Most colonies are healthy. (b) During the heatwave, species-specific susceptibility and local environmental conditions produce heterogeneous responses across sites or species. (c) Post-stress: two possible trajectories for surviving (live) colonies: recovery (top panel), where stressed colonies return toward the healthy vertex; or the stress-legacy (bottom panel), where stressed colonies continue to die, and the dead proportion increases. Because dead colonies cannot revert to living tissue, the proportion of dead colonies does not decrease over the post-stress interval (except through long-term processes such as removal, burial, or recruitment of new colonies)

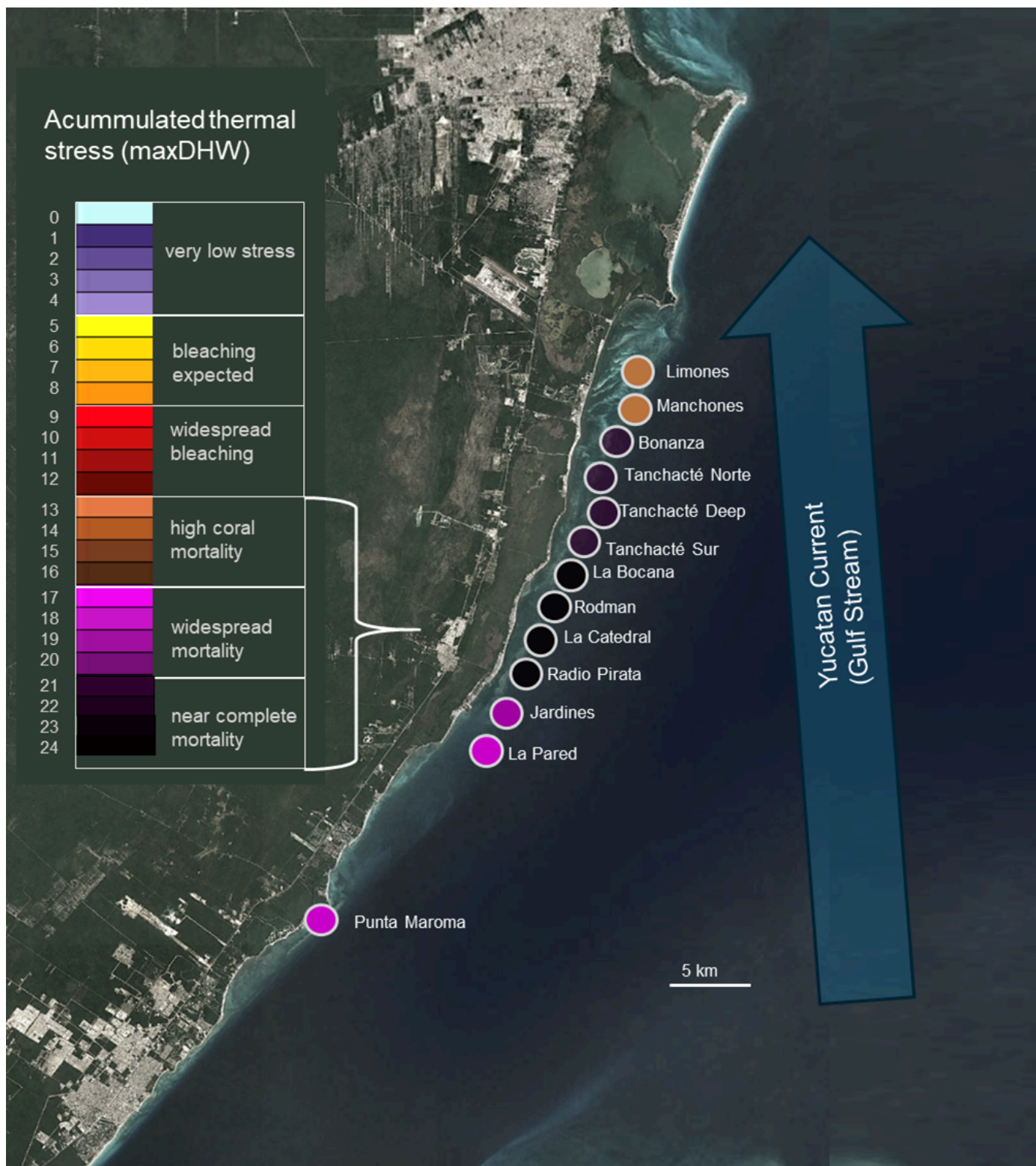


Figure 2

Spatial pattern of accumulated thermal stress (maximum Degree Heating Weeks, maxDHW) across the Puerto Morelos fringing-reef system. Colored circles mark survey sites (labels adjacent) and their corresponding maxDHW class. The translucent arrow indicates the general direction of the Yucatán Current

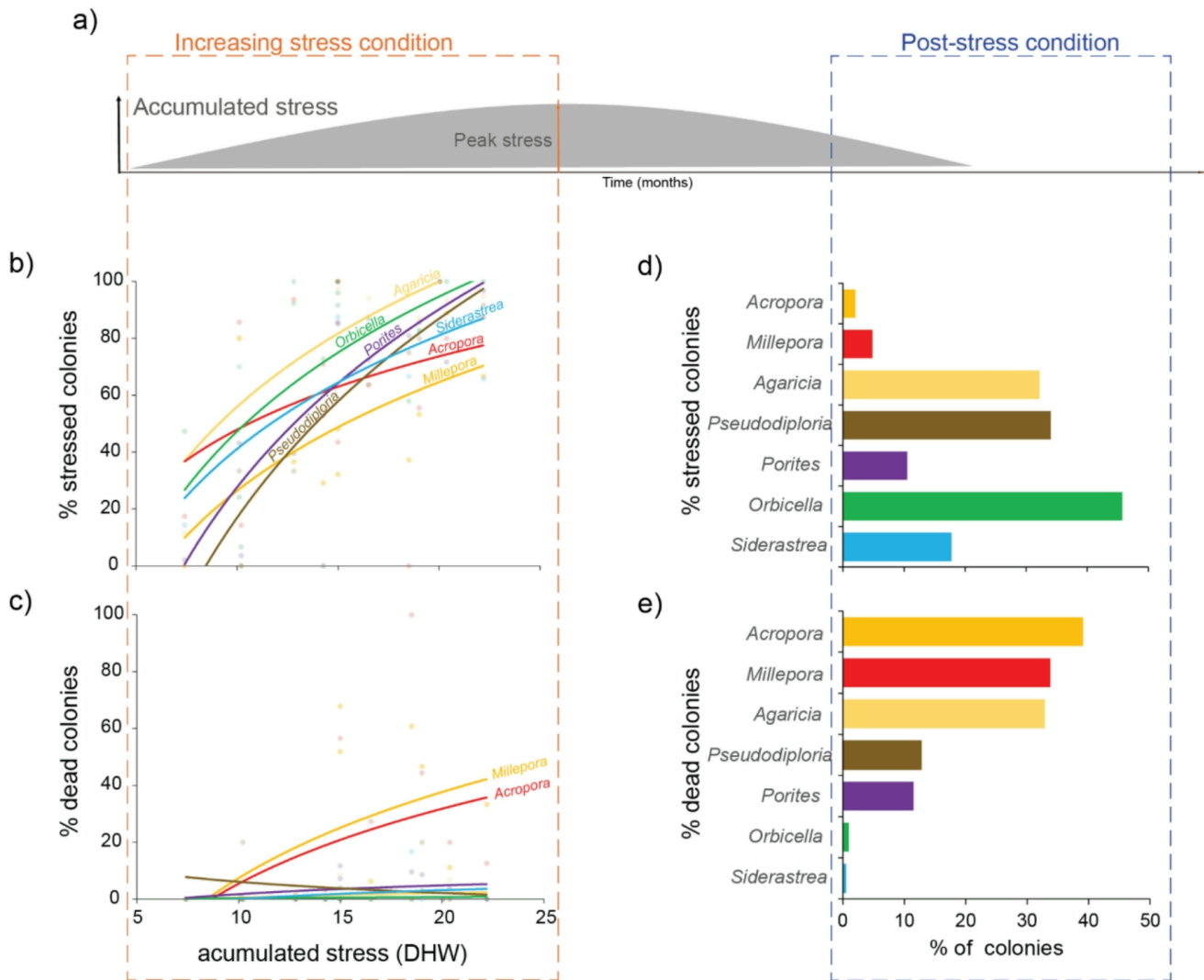
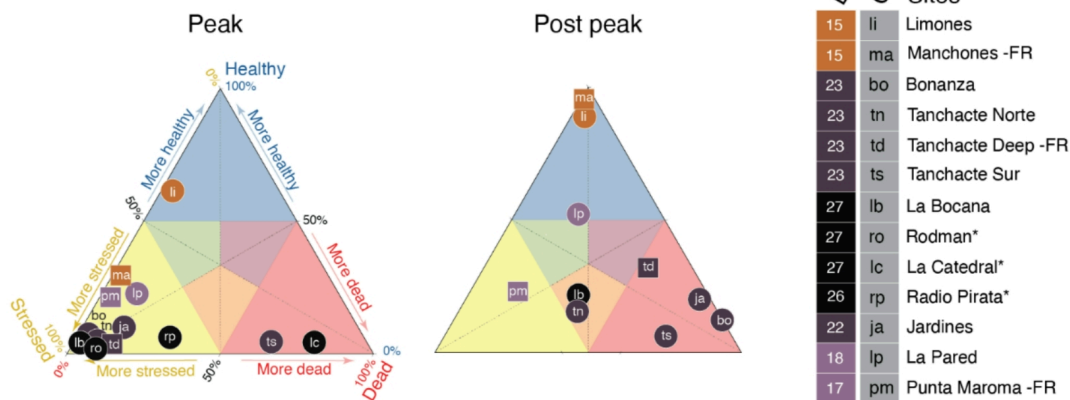


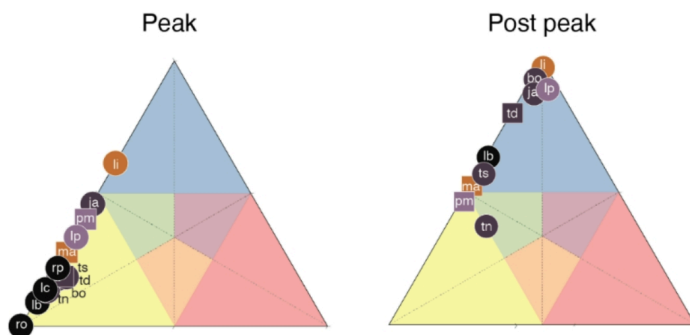
Figure 3

Genera-specific responses to increasing levels of accumulated thermal stress during the 2023 heatwave and resulting post-stress condition. (a) Schematic timeline showing increasing stress from May to October 2023 (orange dashed line) through peak stress and the post-stress observation window (blue dashed line) from December 2023 to February 2024. The relationship between the percentage of stressed (b) and dead (c) colonies for each coral genus as a function of the accumulated stress depicted by the Degree Heating Weeks (DHW) is shown for the increasing stress condition period. Colored lines are fitted species-specific curves, and dots are site-level observations for each genus. (d–e) Post-stress condition: proportion of colonies recorded as stressed (d) and dead (e) by species across surveyed reefs. Species colours are consistent across panels, and labels indicate taxa with sufficient sample size

a) Vulnerable species (*Acropora*, *Agaricia*, *Millepora*)



b) Thermally tolerant reef-building (*Orbicella*, *Pseudiploria*, *Siderastrea*, *Diploria*, *Colpophyllia*, *Montastrea*)



c) Thermally tolerant weedy species (*Isophyllia*, *Madracis*, *Porites*, *Mycetophyllia*, *Dichocoenia*, *Heliocoris*, *Stephanocoenia*)

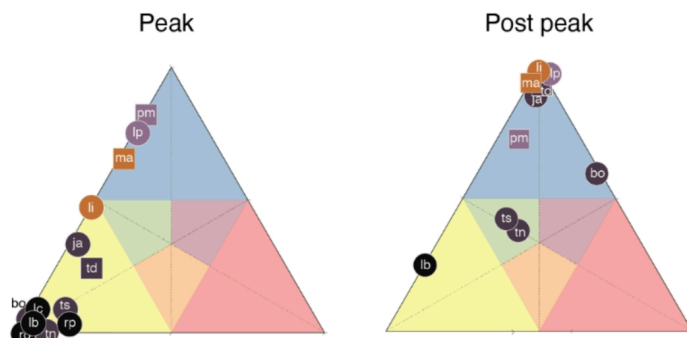


Figure 4

Pathways of change followed by corals at sites with different regimes of thermal stress. Ternary representation of coral community state (proportion healthy, stressed/bleached, dead) across sites and periods (as shown in Fig. 3a). Points represent site-level proportions (label = site code); point fill indicates max Degree Heating Weeks (legend at right) and shape indicates reef type: fore-reef (squares) and back-reefs (circles). Each triangle is a ternary plot with vertices: healthy (top), stressed/bleached

(left), dead (right). Colored background polygons mark compositional regions (e.g., recovery-favoured, high-mortality). Each panel indicates the state of coral colonies during peak (left) and post-peak (right) conditions for three groups of species: vulnerable (a), thermally tolerant reef-building species (b), and thermally tolerant weedy species (c). Species considered in each group are listed in the panel

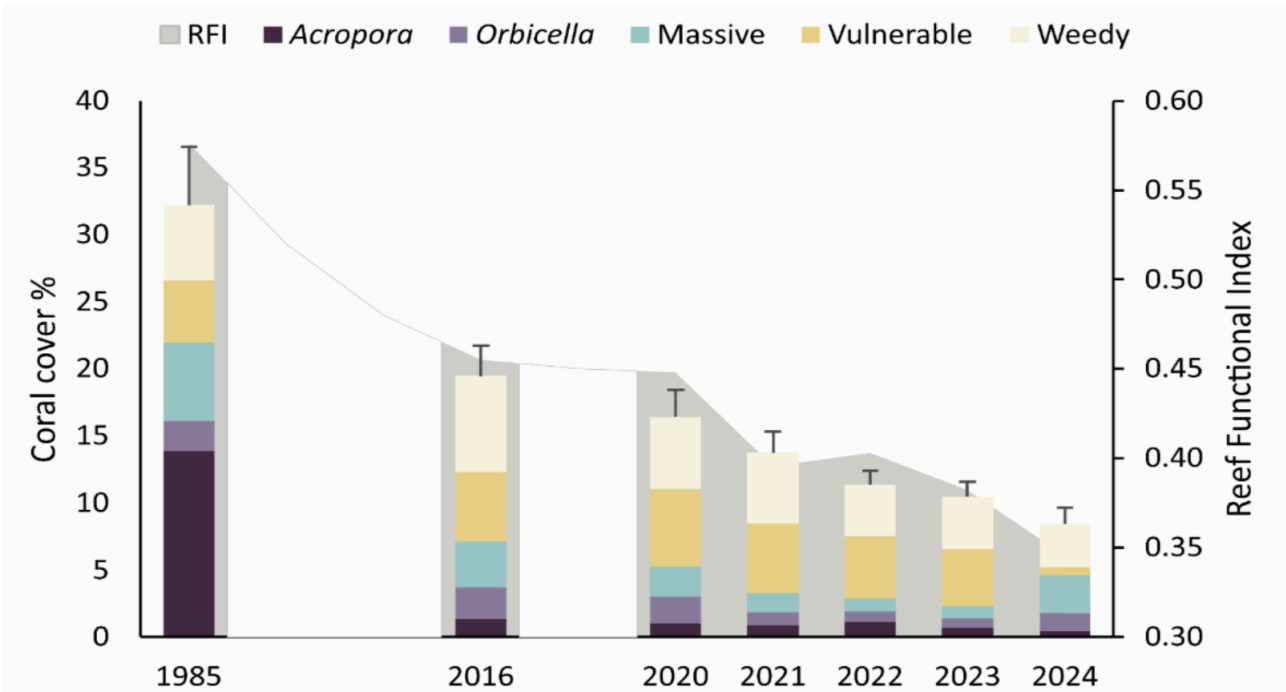


Figure 5

Temporal change (1985–2024) in coral community composition and reef functional capacity (RFI) at eight monitored sites in Puerto Morelos. Stacked bar plots show the mean coral cover (%), with colours within the bars representing the relative abundance of each group: *Acropora* sp., *Orbicella* sp., massive, vulnerable (*Agaricia* and *Millepora*), and weedy corals. Vertical error bars indicate the standard error. The grey line denotes the Reef Functional Index (RFI), a composite indicator of reef structural and ecological functionality