SUPPLEMENT

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Extreme flooding, water quality and mass bleaching compounded impacts in wild and restored Elkhorn coral (*Acropora palmata*) populations in contrasting urban coral reefs in Puerto Rico

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ABSTRACT

Introduction: Recurrent marine heatwaves, stronger hurricanes, and degraded water quality represent increasingly compounded threats to Caribbean coral reefs. These stressors may compromise the persistence of wild endangered Elkhorn coral (*Acropora palmata*) populations and the demographic performance of restored populations.

Objectives: This study examined three climate-driven impact scenarios affecting *A. palmata* in Puerto Rico: (1) extreme rainfall and flooding from Tropical Storm Isaías affecting wild *A. palmata* colonies at the urban reef of El Escambrón; (2) compounded bleaching events during 2023–2024 affecting restored colonies at El Escambrón; and (3) the 2024 bleaching event affecting restored colonies at Punta Melones, Culebra, previously fragmented by Hurricane Beryl.

Methods: Case 1 used line photo-transects from El Escambrón (2005-2022) to assess long-term spatial and temporal changes in benthic community structure and wild *A. palmata* populations. Cases 2 and 3 monitored restored colonies monthly across ten replicate plots per site, measuring survival, live tissue cover, size metrics, and colony condition. Coral metrics were correlated with water quality parameters.

Results: Across El Escambrón and Punta Melones, *A. palmata* colonies experienced catastrophic mortality of 98–100% associated with recurrent thermal stress, low-salinity urban runoff pulses, and compounded bleaching. Sea surface temperature anomaly, 2024 Bleaching Alert Level 4 conditions, chlorophyll-*a*, particulate organic carbon, and dissolved oxygen were significantly associated with mortality.

Conclusions: Coral mortality reflects combined acute and chronic stressors, especially in shallow reefs with degraded water quality and reduced thermal tolerance. With limited recruitment, increasing colony isolation, and low genetic diversity, the species may approach functional extinction without a refugia-based restoration framework.

Key words: *Acropora palmata*; marine heatwaves; mass bleaching; mortality; restoration.

RESUMEN

Impactos compuestos de inundaciones extremas, calidad de agua y blanqueamiento masivo en poblaciones de coral cuerno de alce (*Acropora palmata*) silvestres y restaurados en arrecifes de coral urbanos contrastantes en Puerto Rico

Introducción: Las olas recurrentes de calor marinas, los huracanes más intensos y el deterioro de la calidad del agua representan amenazas cada vez más complejas para los arrecifes de coral del Caribe. Estos factores de estrés pueden comprometer la supervivencia de las poblaciones silvestres de coral cuerno de alce (*Acropora palmata*), en peligro de extinción, y el desempeño demográfico de las poblaciones restauradas.

Objetivos: Este estudio examinó tres escenarios de impacto climático que afectan a *A. palmata* en Puerto Rico: (1) lluvias extremas e inundaciones provocadas por la tormenta tropical Isaías que afectaron a las colonias silvestres de *A. palmata* en el arrecife urbano de El Escambrón; (2) eventos de blanqueamiento combinados durante 2023–2024 que afectaron a las colonias restauradas en El Escambrón; y (3) el evento de blanqueamiento de 2024 que afectó a las colonias restauradas en Punta Melones, Culebra, previamente fragmentadas por el huracán Beryl.

Métodos: El caso 1 utilizó transectos fotográficos lineales de El Escambrón (2005-2022) para evaluar los cambios espaciales y temporales a largo plazo en la estructura de la comunidad bentónica y las poblaciones silvestres de *A. palmata*. En los casos 2 y 3, se realizó un seguimiento mensual de las colonias restauradas en diez parcelas replicadas por sitio, midiendo la supervivencia, la cobertura de tejido vivo, las métricas de tamaño y el estado de las colonias. Las métricas de los corales se correlacionaron con los parámetros de calidad del agua.

Resultados: En El Escambrón y Punta Melones, las colonias de *A. palmata* experimentaron una mortalidad catastrófica del 98-100% asociada con estrés térmico recurrente, pulsos de escorrentía urbana de baja salinidad y blanqueamiento compuesto. La anomalía de la temperatura superficial del mar, las condiciones de nivel de alerta de blanqueamiento 4 de 2024, la clorofila-*a*, el carbono orgánico particulado y el oxígeno disuelto se asociaron significativamente con la mortalidad.

Conclusiones: La mortalidad de los corales refleja la combinación de factores de estrés agudos y crónicos, especialmente en arrecifes someros con calidad del agua degradada y tolerancia térmica reducida. Con un reclutamiento limitado, un creciente aislamiento de las colonias y una baja diversidad genética, la especie podría acercarse a la extinción funcional sin un marco de restauración basado en refugios.

Palabras clave: *Acropora palmata*; blanqueamiento masivo; mortalidad; olas de calor marino; restauración.

INTRODUCTION

Coral reefs are rapidly declining worldwide, including the wider Caribbean, due to multiple compounded anthropogenic stressors (Wilkinson & Souter, 2008). Local impacts such as declining water quality, sedimentation, turbidity, eutrophication (Cloern, 2001), and overfishing (Jackson et al., 2014), compounded with regional and global drivers like extreme heat and ocean acidification, reduce light availability and intensify chronic stress. These conditions, together with recurrent marine heatwaves, have led to long-term reductions in coral cover and growth (Gardner et al., 2003; Wilson et al., 2010). Projected widespread warming across the wider Caribbean and eastern tropical Pacific suggests mounting challenges for future coral reef conservation and restoration efforts (Hernández-Delgado, 2015; Hernández-Delgado & Rodríguez-González, 2025).

Acropora palmata was historically the dominant branching coral on shallow, wave-exposed Caribbean reefs (Glynn, 1973; Goreau, 1959; Milliman, 1973), including Puerto Rico (Fig 1A). Its rapid growth, ability to reproduce sexually and asexually, and capacity to create large, complex branching frameworks made it a keystone species (Bruckner, 2002; Bruckner & Hourigan, 2000; Rodríguez-Martínez et al., 2014). Colonies can reach 2–3 m branch lengths and 4–8 m diameters, with growth rates of 5–9.5 cm·yr−1 (Díaz-Ortega & Hernández-Delgado, 2014). The species thrives in clear, well-circulated waters and moderate temperatures (25–29°C). However, *A. palmata* has undergone severe regional declines due to chronic compounded anthropogenic stress, hurricanes, and climate-driven bleaching and mortality (Díaz-Ortega & Hernández-Delgado, 2014; Hernández-Delgado et al., 2010a; Hernández-Delgado et al., 2010b; Hernández-Delgado et

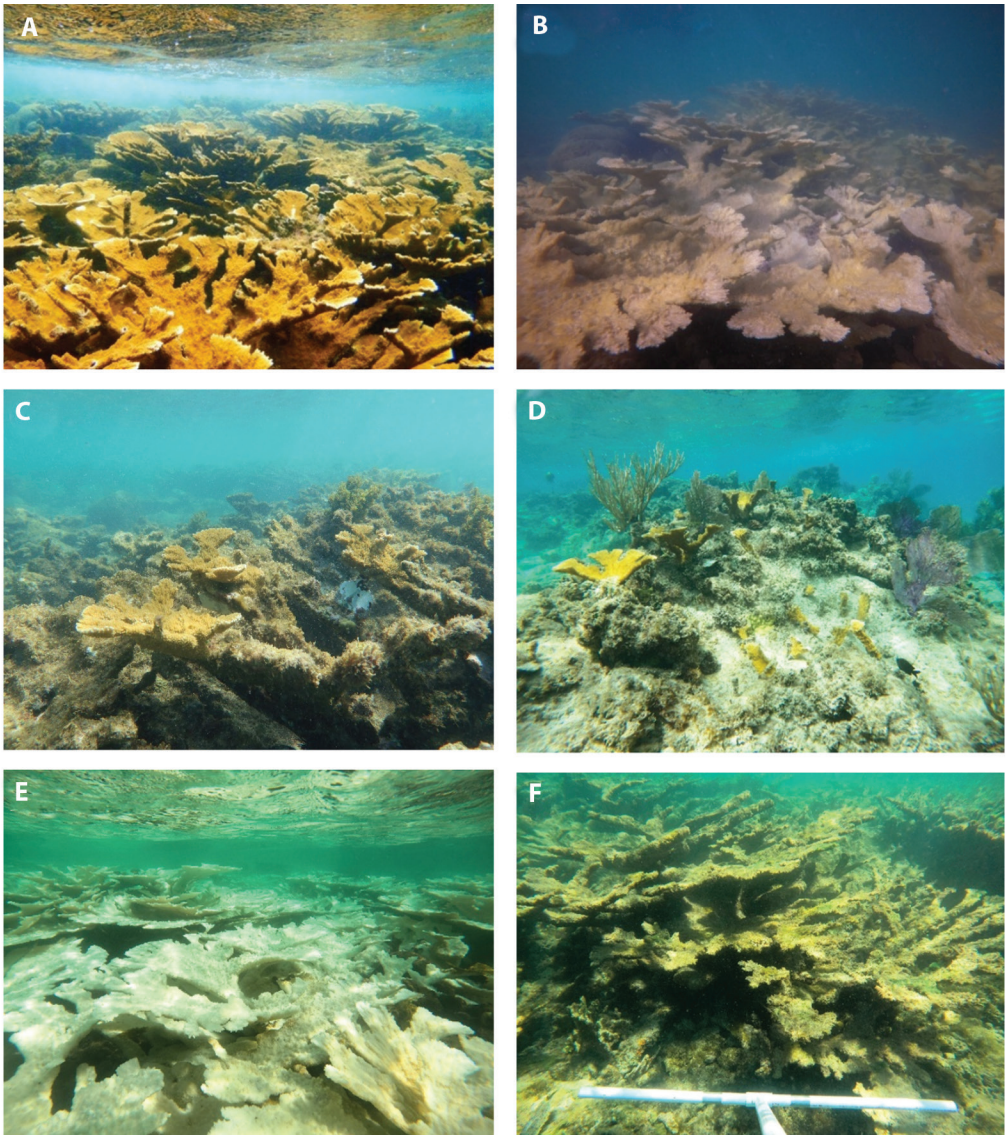

Fig. 1. Examples of the multiple stages of *Acropora palmata* populations in Puerto Rico between 2020 and 2024. **A.** High coverage of *A. palmata* stands at El Escambrón urban reef prior to tropical storm Isaías (2020). **B.** Total mortality of *A. palmata* following extreme rainfall and mass flooding impacts following tropical storm Isaías. **C.** Detail of restored *A. palmata* assemblages at El Escambrón (2024) prior to mass coral bleaching, **D.** Detail of replanted *A. palmata* colonies at Punta Melones, Culebra Island (previously restored and dislodged by bottom swells generated by Hurricane Beryl) prior to mass coral bleaching (2024). **E.** Mass coral bleaching affecting 15-year old restored *A. palmata* during 2024, **F.** Post-bleaching mass mortality of old restored *A. palmata*.

al., 2024; Manzello et al., 2025). It was listed as threatened under the U.S. Endangered Species Act in 2006 (Weijerman et al., 2014), and its critical habitat was designated in 2008 as shallow (< 30 m) reef structures and pavements. As a result of its widespread decline, extensive conservation and restoration efforts have been implemented across the region.

The wider Caribbean has low coral functional redundancy relative to the Indo-Pacific (Bellwood et al., 2004). *Acropora palmata* is the only large, fast-growing branching species capable of generating high structural complexity and dominating shallow, high-energy zones. It is therefore central to coral restoration efforts, enhancing habitat heterogeneity for fishes and invertebrates (Hernández-Delgado & Laureano, 2024; Huntington et al., 2017). Additionally, its robust frameworks help dissipate wave energy, protect shorelines, support nursery habitats, and sustain coastal productivity and socio-economic value across the region (Familkhalili et al., 2025; Osorio-Cano et al., 2019; Reguero et al., 2018).

Mounting human activities along urban coasts have significantly contributed to the decline of *A. palmata*, including chronic sedimentation, turbidity, sewage pollution, eutrophication, solid waste, oil spills, and urban runoff (Díaz-Ortega & Hernández-Delgado, 2014; Hernández-Delgado et al., 2010b; Rogers, 1990). Additional shoreline alterations—beach armoring, storm sewer construction, water diversion, dredging, filling, and beach renourishment—further degrade shallow reefs (Hernández-Delgado & Rosado-Matías, 2017; Hernández-Delgado et al., 2010a). Numerous studies in Puerto Rico document chronic turbidity, water quality decline, sewage contamination, and sedimentation impacting benthic communities and coral resilience near urbanized coasts (Bonkosky et al., 2009; Gómez-Andújar & Hernández-Delgado, 2020; Hernández-Delgado et al., 2010a; Hernández-Delgado et al., 2010b; Otaño-Cruz et al., 2017; Otaño-Cruz et al., 2019; Ramos-Scharrón et al., 2012; Ramos-Scharrón et al., 2015).

Projected warming trends are expected to magnify extreme rainfall, hurricanes, prolonged heatwaves, and mass bleaching, further threatening shallow coral persistence through a combination of compounded impacts (Hernández-Delgado & Rodríguez-González, 2025; Manzello et al., 2025). Extreme rainfall events can deliver sediment- and nutrient-laden runoff that can cause extensive Acroporid mortality (Hernández-Delgado et al., 2014a). Tropical storm Isaías (July 2020) produced ~25–30 cm of rainfall in 24 hours, triggering major coastal flooding in San Juan and discharging turbid, hypoxic waters that killed most *A. palmata* colonies at El Escambrón (Fig. 1B) (Hernández-Delgado et al., 2020). Similarly, powerful swells from Category 5 Hurricane Beryl (June 2024) dislodged and fragmented restored colonies at Punta Melones, Culebra Island. Climate change has led to increased prevalence of bleaching conditions across the wider Caribbean and to increased risks of extreme weather events, potentially enhancing coral reefs vulnerability of exposure to compounded environmental stressors.

In response, community-based restoration efforts were launched. In 2023, Sociedad Ambiente Marino (SAM) and Grupo VIDAS transplanted 500 resilient *A. palmata* clippings from Vega Baja reefs to El Escambrón in San Juan, shortly before a mass bleaching event (Fig. 1C). In Culebra, SAM similarly reattached 300 fragments in July 2024, following Hurricane Beryl (Fig. 1D). Afterwards, the unprecedented compounded extreme heat and bleaching event in 2024 nearly eliminated wild and restored populations (Fig. 1E, Fig. 1F).

Natural recovery of *A. palmata* through sexual larval recruitment has been extremely limited or absent across many Caribbean sites following major hurricanes and environmental disturbances (González-Figueroa & Hernández-Delgado, 2021; Hernández-Delgado & Ortiz-Flores, 2022; Hernández-Delgado et al., 2014b; Hernández-Delgado et al., 2024). As a result, ecological restoration has become essential for rebuilding depleted populations, restoring reef accretion, enhancing fish habitat, and supporting long-term wave attenuation (Hernández-Delgado et al., 2018a; Hernández-Delgado et al., 2018b; Hernández-Delgado, 2024). This study examined three compounded climate-driven extreme events affecting wild and restored *A. palmata*: extreme rainfall and runoff, unprecedented early-summer hurricane swells, and two consecutive marine heatwaves and mass bleaching events. Coral demographic

responses were evaluated alongside remotely sensed water-quality parameters to understand potential relationships.

The following research questions were addressed: (1) What was the long-term impact of compounded coral bleaching events and extreme rainfall and runoff on coral reef benthic community structure at El Escambrón beach, San Juan?; (2) What was the impact of compounded mass coral bleaching events in 2023 and 2024 and coastal water quality on the demographic performance of restored *A. palmata* at El Escambrón?; (3) What was the compounded impact of bottom swells from category five Hurricane Berryl and the 2024 mass coral bleaching event on the demographic performance of restored *A. palmata* at Punta Melones, Culebra Island? This allowed testing three hypotheses: (1) Extreme rainfall and runoff can lead to significant coral mortality and regime shifts in coral reef benthic community structure; (2) Compounded marine heatwaves, mass coral bleaching and declining water quality are strongly correlated to restored *A. palmata* mortality; (3) Compounded mass coral bleaching can lead to mortality of restored hurricane-dislodged *A. palmata* fragments. Findings of this study provide critical guidance for reef managers and restoration practitioners facing escalating climate-related stressors in the Anthropocene.

MATERIALS AND METHODS

We feature three case studies highlighting a combination of compounded impacts: (1) extreme rainfall and runoff impacts on coral reef benthic assemblages and on a wild *A. palmata* populations at three zones of El Escambrón, San Juan; (2) the compounded mass bleaching events in 2023 and 2024, combined with water quality effects, on a restored *A. palmata* demographic performance at El Escambrón; and (3) the compounded 2024 mass bleaching impacts and water heat stress on a hurricane-fragmented, restored *A. palmata* population at Punta Melones, Culebra Island.

Study sites

Case study 1 – El Escambrón (Benthic community and wild A. palmata population): Arrecife La Ocho at El Escambrón is a shallow (< 3 m), wave-exposed urban reef located 250–350 m offshore in San Juan. This is a high-energy, exposed, shallow linear reef system along the northern coast of Puerto Rico exposed to recurrent North Atlantic swells. Despite chronic human pressures, it historically supported extensive *A. palmata* frameworks (Fig. 1A). Long-term monitoring quantified changes in benthic community composition at increasing time intervals between 2005 and 2022 across east (18.469415°, −66.090060), middle (18.469306°, −66.090806), and west (18.469456°, −66.091565) backreef zones (1.5–2.5 m) behind Arrecife La Ocho. The site experienced significant mass coral bleaching in 2005, 2010, 2019, 2021, 2023 and 2024, as well as a severe sediment-laden, nutrient-loaded large-scale runoff pulse impact during flooding associated with tropical storm Isaías (July 27–28, 2020), when ~30 cm of rainfall in 24 hours discharged turbid, hypoxic floodwaters that caused mass mortality of corals, fish, and invertebrates (Hernández-Delgado et al., 2020).

Case study 2 – El Escambrón (Restored A. palmata population): A total of 500 *A. palmata* clippings from Vega Baja, 33 km west of San Juan, were out-planted in June 2023 onto the backreef shallow (1–1.5 m) coral framework at El Escambrón (18.469098°, −66.090796°), an area formerly dominated by monotypic *A.palmata* stands that were decimated by the 2020 flood event and showed no natural recovery for at least three years. Fragments were attached to dead-standing coral branches using plastic ties across 50 replicate ~10 m^2 plots of 10 out-plants each. A total of 100 colonies were tagged and geo-referenced for long-term monitoring.

Case study 3 – Punta Melones, Culebra (Restored A. palmata population): Punta Melones, located within the Canal Luis Peña Natural

Reserve (18.305722°, −65.312512°), is a shallow (1–4 m) linear reef along Culebra's leeward coast, 28 km east of Puerto Rico. The site supports diverse coral assemblages and extensive restored *A. palmata* populations. Swells from Category 5 Hurricane Beryl (June 27, 2024) caused significant fragmentation and dislodgment of wild and restored colonies. In August 2024, 300 fragments were reattached to the backreef substrate (1-1.5 m) using masonry nails and plastic ties across 30 replicate ~10 m^2 plots, and 100 colonies were tagged and georeferenced for long-term monitoring.

Sampling design

Case study 1: Spatio-temporal variation in benthic community structure and wild *A. palmata* demographic performance at El Escambrón was quantified across east, middle, and west backreef zones behind high-energy Arrecife La Ocho using six replicate georeferenced 10 m haphazard photo-transects per zone (five 75 × 50 cm haphazard quadrats each). Surveys were conducted in 2005, 2007, 2008, 2012, 2015, 2018, 2020, and 2022 measuring percent cover of corals, sponges, zoanthids, algal groups, and open substrates, as well as coral species richness, Shannon-Weaver diversity index (H'c), and evenness (J'c). Water-quality conditions during and after the 2020 flood event were recorded at 5-second intervals using HOBO U24 (conductivity–salinity) and U26 (dissolved oxygen) loggers (Onset Computers), with 70–275 readings per site. Variables measured included temperature, salinity, conductivity, and dissolved oxygen.

Spatio-temporal variation in benthic community structure was analyzed using a two-way permutational analysis of variance (PERMANOVA), with time and reef zone as main variables, and transects as the error term, using √-transformed data (Anderson et al., 2008). Community trajectories were visualized using principal coordinates ordination (PCO), variation in species dominance was projected using cumulative dominance plots, changes in coral beta diversity were documented using permutational dispersion analysis (PERMDISP), and variation patterns in indicator taxa were determined using similarity percentages analysis (SIMPER) following Clarke et al. (2014). Water-quality variation following the 2020 flooding event was analyzed with two-way PERMANOVA (time × location; replicate readings as error term). $Log_{10}(x+1)$-transformed and normalized data were examined using principal components analysis (PCA) (Clarke et al., 2014). All multivariate tests used 9 999 permutations. This sampling design allowed comparing impacts of the prior mass bleaching events and the 2020 mass flooding event to test the hypothesis of stronger mass flooding and runoff impacts on coral demographic performance.

Case study 2: Spatio-temporal variation in restored *A. palmata* demographic performance was assessed using 500 clippings transplanted from Vega Baja to El Escambrón back reef in June 2023. Survival and growth of 100 permanently tagged colonies were monitored monthly from June to October 2023 and quarterly from February to November 2024, spanning the 2023–2024 compounded bleaching events. Colonies were distributed across ten replicate ~10 m^2 plots (10 colonies per plot, spaced 3–5 m apart). Maximum length, height, surface area, and volume were measured *in situ* using a calibrated tape. Percent live tissue cover and colony condition (i.e., bleached, diseased, unblemished) were also determined.

Remotely sensed water-quality variables—including diffuse attenuation coefficient (Kd_{490}), photoactive radiation (PAR), suspended particulate matter concentration (SPM), sea surface temperature (SST), sea surface temperature anomaly (SSTa), hot spot (HS), degree heating weeks (DHWs), salinity (sss), net primary productivity (NPP), chlorophyll-*a* concentration, particulate inorganic carbon concentration (PIC), particulate organic carbon concentration (POC), the NAVGEM 10 m wind (east-west, north-south components), sea surface current east-west (UGOS) and north-south (VGOS) components, and bleaching

alerts—were obtained from NOAA NMFS SWFSC ERDAPP (ERDDAP-NOAA, 2024) for the period of June 2023 to November 2024. Data were extracted from a 2 km area approximately 1.5 km offshore on each location to avoid technical limitations of remotely sensed data from shallow reef zones.

Demographic variation was analyzed using two-way PERMANOVA (time × plot), with √-transformed colony surface area visualized using PCO. Water-quality variation was assessed using $Log_{10}(x+1)$-transformed, normalized data and illustrated with PCA. Multivariate correlation (RELATE) was used to test correlations between coral demographic performance and the water-quality matrix, and BEST/BIOENV identified environmental variables best explaining temporal changes in colony surface area (Clarke et al., 2014) following compounded bleaching impacts. All multivariate tests used 9 999 permutations.

Case study 3: A total of 300 storm-generated *A. palmata* fragments from original restored colonies were collected at Punta Melones in August 2024 after 3–4 m long-period (14 seconds) swells from Category 5 Hurricane Beryl (June 27, 2024). Fragments were reattached at 1–1.5 m depth backreef and forereef areas. Survival and growth of 100 permanently tagged colonies were monitored monthly from August 2024 to January 2025 throughout the 2024 mass bleaching event. Colonies were distributed across ten replicate ~10 m^2 plots (10 colonies per plot, spaced 5–10 m apart). Maximum length, height, surface area, volume, percentage live tissue cover, and colony condition were determined as described above. Bleaching index was determined using a semi-quantitative scale: 0 = No bleaching; 1 = Colony paling; 2 = Mostly bleaching; 3 = Patchy bleaching; 4 = Nearly total bleaching; 5 = Total bleaching. Remotely sensed SST, SSTa, HS, and DHWs for the same period were obtained as described above.

Demographic variation was analyzed using two-way PERMANOVA (time × plot), with √-transformed surface area visualized using PCO. Water-quality variation was assessed using $Log_{10}(x+1)$-transformed, normalized data and illustrated with PCA. RELATE tested correlations between colony performance and water-quality patterns, while BEST/BIOENV identified variables best explaining temporal changes in surface area. All multivariate analyses used 9 999 permutations.

RESULTS

Case study 1– Long-term spatio-temporal variation in benthic community structure at El Escambrón: PCO revealed significant benthic community persistence between 2005 and 2015, followed by minor changes in 2018 (after category five Hurricane María in 2017), followed by strong spatio-temporal variation in benthic community structure, with pronounced regime shifts following the 2020 extreme rainfall and runoff event and associated mass mortality (Fig. 2). Clear clustering patterns occurred at each reef zone, indicating distinct disturbance histories. The eastern site reflected moderate impacts from the 2008 winter swells, Hurricane María (2017), then stronger impacts from tropical storm Isaías (2020), and the 2021 SCTLD outbreak that resulted in a significant change in community trajectory. The western site showed a similar trajectory, while the middle site—formerly dominated by *A. palmata*—showed high temporal persistence between 2005 and 2018 but was strongly affected by Isaías. These patterns corresponded to highly significant ($p < 0.0001$) spatial and temporal variation in benthic community structure, with significant interaction effects (Table 1).

Cumulative species dominance plots showed overall long-term community persistence but further illustrated temporal shifts after the 2020 runoff event and highlighted SCTLD-driven declines of *Pseudodiploria strigosa* and other massive corals between 2020–2022, intensifying algal proliferation and altering overall community structure (Fig. 3).

There was a highly significant spatio-temporal decline in live coral cover, with a strong time × location interaction ($p < 0.0001$)

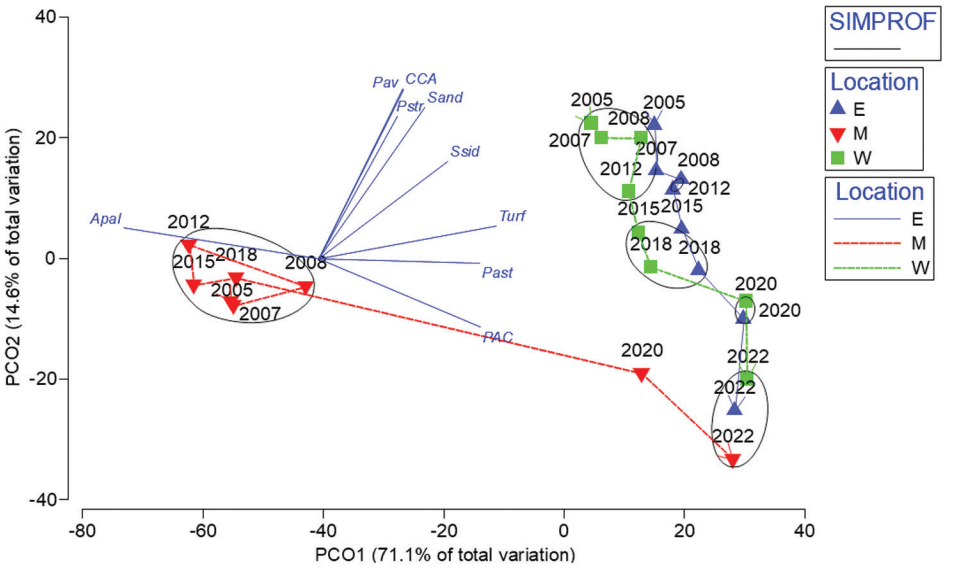

Fig. 2. Principal coordinates ordination (PCO) of the spatio-temporal variation in coral reef benthic community structure at El Escambrón reef. This solution explains 85.7 % of the observed variation.

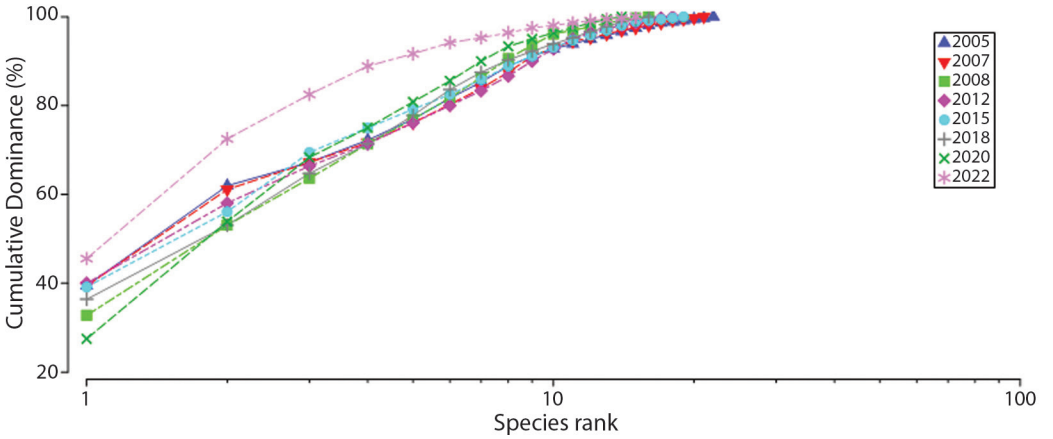

Fig. 3. Cumulative species analysis of temporal variation in benthic community structure at El Escambrón based on √-transformed averaged data across replicate reef sites.

(Fig. 4A, Table 1). *Acropora palmata* showed an equally significant decline ($p < 0.0001$) following the flooding event (Fig. 4B). *Acropora cervicornis* exhibited a non-significant decrease (Fig. 4C), while *A. prolifera* showed a non-significant loss but significant spatial variation ($p = 0.0080$) (Fig. 4D). *Pseudodiploria strigosa* declined significantly over time ($p < 0.0001$) and varied spatially ($p < 0.0001$), with no interaction effect (Fig. 4E). Observed decline in *P. strigosa* coincided with the compounded impacts of the SCTLD outbreak and the runoff event. In contrast, *Porites astreoides* increased significantly over time ($p = 0.0002$) and varied spatially ($p < 0.0001$), with no significant interaction (Fig 4F).

Table 1
Two-way permutational analysis of variance (PERMANOVA) results of spatio-temporal variation in coral reef benthic community structure and indicator coral species at El Escambrón reef (2005–2022).

Source	df	Pseudo-F	P(perm)	Unique perms	√-Estimate of components of variation
Community structure					
Time	7	35.15	< 0.0001	9 919	24.39
Location	2	162.48	< 0.0001	9 934	32.48
Time x Location	14	8.09	< 0.0001	9 881	19.24
% Coral					
Time	7	44.09	< 0.0001	9 929	14.14
Location	2	88.50	< 0.0001	9 942	12.34
Time x Location	14	15.55	< 0.0001	9 904	14.24
% *Acropora palmata*					
Time	7	74.76	< 0.0001	9 956	28.35
Location	2	106.43	< 0.0001	9 956	20.76
Time x Location	14	5.56	< 0.0001	9 900	12.21
% *Acropora cervicornis*					
Time	7	0.89	0.5339	9 956	-0.78
Location	2	2.60	0.0706	9 956	1.80
Time x Location	14	0.54	0.9353	9 900	-2.71
% *Acropora prolifera*					
Time	7	1.71	0.1071	9 910	2.85
Location	2	4.91	0.0080	9 939	4.09
Time x Location	14	1.35	0.1799	9 932	3.4z5
% *Pseudodiploria strigosa*					
Time	7	6.91	< 0.0001	9 947	12.06
Location	2	27.40	< 0.0001	9 965	15.61
Time x Location	14	0.59	0.8726	9 935	-5.49
% *Porites astreoides*					
Time	7	5.19	0.0002	9 945	8.42
Location	2	88.36	< 0.0001	9 943	23.55
Time x Location	14	1.46	0.1315	9 920	4.82

There were highly significant spatial differences ($p < 0.0001$) and a strong temporal increase ($p < 0.0001$) in macroalgal cover, with a significant time × location interaction ($p = 0.0002$) (Fig. 5A, Table 2). Similar spatio-temporal patterns occurred for algal turf ($p < 0.0001$) (Fig. 5B), *Peyssonnelia* algal crusts (PAC) ($p < 0.0001$) (Fig. 5C), and red encrusting algae, *Ramicrusta textilis* ($p < 0.0001$) (Fig. 5D). Crustose coralline algae (CCA) showed a significant temporal decline ($p < 0.0001$), strong spatial variation ($p < 0.0001$), and significant interaction effects ($p = 0.0025$) (Fig. 5E). Cyanobacteria increased significantly over time ($p < 0.0001$), showed no spatial differences, but exhibited significant time × location interactions ($p = 0.0004$) (Fig. 5F).

Coral species richness (S) declined sharply after the 2020 mass mortality event ($p < 0.0001$) and showed significant spatial variation ($p < 0.0001$), with no time × location interaction (Fig. 6A, Table 3). Coral Shannon-Weaver diversity index (H'c) showed similar significant temporal ($p < 0.0001$) and spatial ($p < 0.0001$) patterns, without interaction effects (Fig. 6B). Coral evenness (J'c) exhibited no significant

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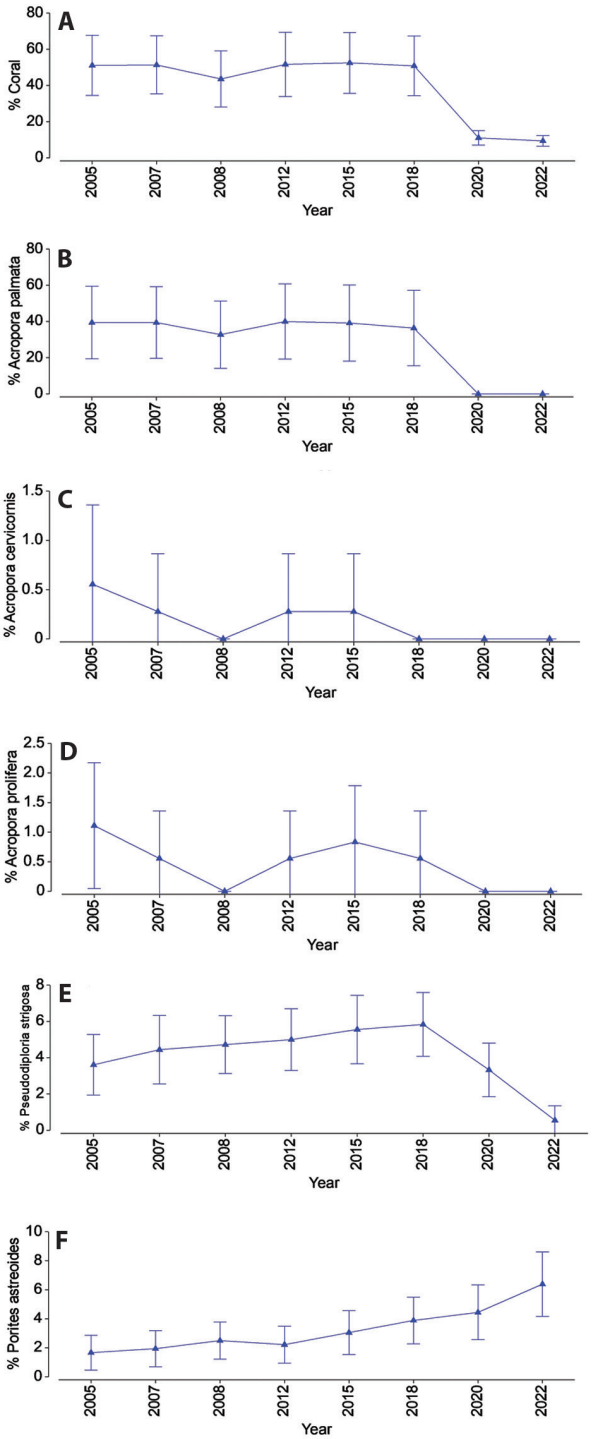

Fig. 4. Temporal variation in coral assemblages at El Escambrón reef. **A.** Percent live coral cover, **B.** Percent *Acropora palmata* cover, **C.** Percent *A. cervicornis* cover, **D.** Percent *A. prolifera* cover, **E.** Percent *Pseudodiploria strigosa* cover, **F.** Percent *Porites astreoides* cover. Means ± standard error.

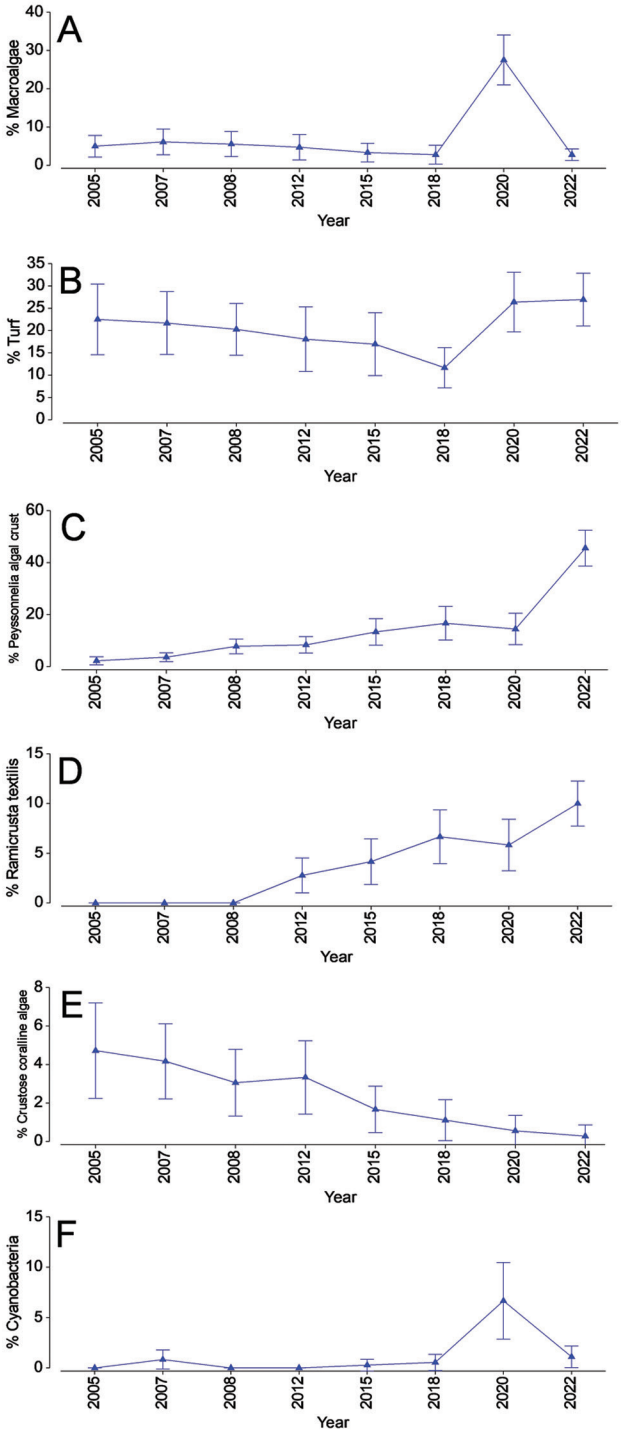

Fig. 5. Temporal variation in algal assemblages at El Escambrón reef: **A.** Percent macroalgae cover, **B.** Percent algal turf cover, **C.** Percent *Peyssonnelia* algal crust (PAC) cover, **D.** Percent *Ramicrusta textilis* cover, **E.** Percent crustose coralline algae (CCA) cover, **F.** Percent cyanobacteria cover. Means ± standard error.

Table 2
Two-way permutational analysis of variance (PERMANOVA) results of spatio-temporal variation in algal assemblages' composition at El Escambrón reef (2005–2022).

Source	df	Pseudo-F	P(perm)	Unique perms	√-Estimate of components of variation
% Macroalgae					
Time	7	11.32	< 0.0001	9 941	15.47
Location	2	44.54	< 0.0001	9 940	18.54
Time x Location	14	3.45	0.0002	9 924	13.06
% Algal turf					
Time	7	10.51	< 0.0001	9 921	9.14
Location	2	118.52	< 0.0001	9 964	19.67
Time x Location	14	12.08	< 0.0001	9 896	17.08
% *Peyssonnelia algal crust*					
Time	7	35.93	< 0.0001	9 945	17.24
Location	2	243.76	< 0.0001	9 945	27.83
Time x Location	14	8.73	< 0.0001	9 921	14.05
% *Ramicrusta textilis*					
Time	7	108.97	< 0.0001	9 930	22.38
Location	2	133.78	< 0.0001	9 949	15.20
Time x Location	14	22.68	< 0.0001	9 929	17.37
% Crustose coralline algae					
Time	7	7.40	< 0.0001	9 935	11.28
Location	2	39.89	< 0.0001	9 942	17.03
Time x Location	14	2.55	0.0025	9 915	9.63
% Cyanobacteria					
Time	7	11.13	< 0.0001	9 946	11.61
Location	2	1.26	0.2855	9 943	1.15
Time x Location	14	3.07	0.0004	9 913	9.09

temporal change but showed strong spatial variation ($p < 0.0001$) and a significant interaction ($p = 0.0165$) (Fig. 6C).

PERMDISP indicated highly significant spatio-temporal shifts in coral beta diversity ($F = 7.68$, d.f. = 23,120, $p < 0.0001$) following runoff impacts. SIMPER analysis using combined annual data from the three reef sites showed that *A. palmata* dominated El Escambrón reef in 2005 (36.1–37.8 %), declining slightly after Hurricane María in 2017 (29.7 %) before collapsing entirely following the 2020 extreme rainfall and runoff event. In 2020, macroalgae (28.3 %), algal turf (27.3 %), and PAC (10.6 %) became dominant, jointly explaining 66.3 % of the observed variation in community structure. By 2022, PAC (38.2 %), turf (27.7 %), and *R. textilis* (16.9 %) dominated, accounting for 82.8 % of the post-disturbance assemblage.

Tropical storm Isaías generated extreme rainfall and runoff that caused mass coral mortality at El Escambrón. PCA revealed strong shifts in the water-quality matrix between samples collected within one week of the storm and those taken a month later (Fig. 7), driven primarily by declining salinity, conductivity, and dissolved oxygen concentration during the runoff event, with smaller contributions from SST. This solution explained 98.5 % of the observed spatio-temporal variation in water quality. Salinity averaged 22.8 ppt immediately after the storm and recovered to 36.0 ppt a month later, showing significant temporal (Pseudo-F = 135080, $p < 0.0001$) and spatial

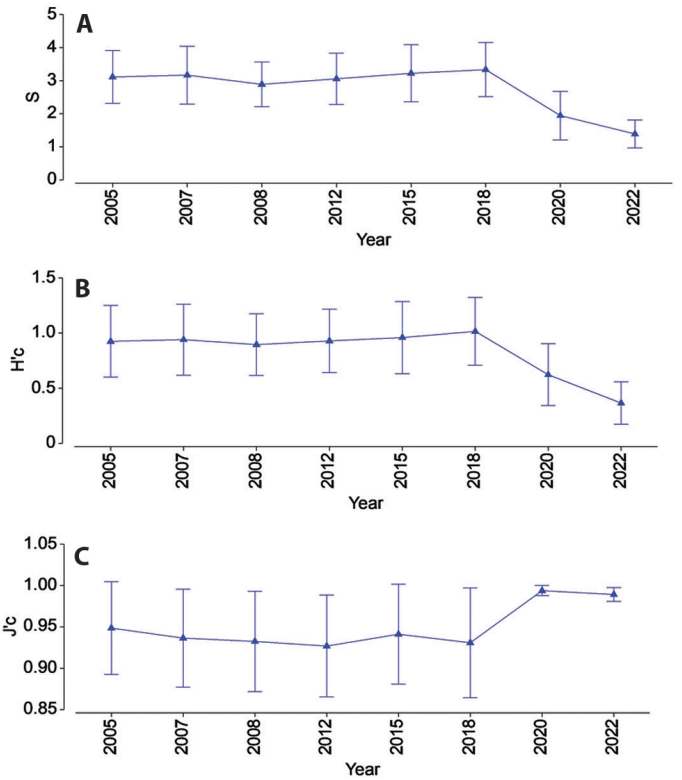

Fig. 6. Temporal variation in coral biodiversity at El Escambrón reef: **A.** Species richness, **B.** Shannon-Weaver species diversity index (H'_c), **C.** Pielou's evenness (J'_c). Means ± standard error.

Table 3

Two-way permutational analysis of variance (PERMANOVA) results of spatio-temporal variation in coral biodiversity at El Escambrón reef (2005–2022).

Source	df	Pseudo-F	P(perm)	Unique perms	√-Estimate of components of variation
Species richness (S)					
Time	7	8.16	< 0.0001	9 940	0.66
Location	2	77.85	< 0.0001	9 943	1.33
Time x Location	14	0.83	0.6222	9 922	-0.17
Species diversity index (H'_c)					
Time	7	7.39	< 0.0001	9 938	0.21
Location	2	126.02	< 0.0001	9 952	0.56
Time x Location	14	1.44	0.1403	9 919	0.09
Evenness (J'_c)					
Time	7	0.94	0.8624	9 946	-0.01
Location	2	1153	< 0.0001	9 971	0.08
Time x Location	14	12.91	0.0165	9 981	0.02

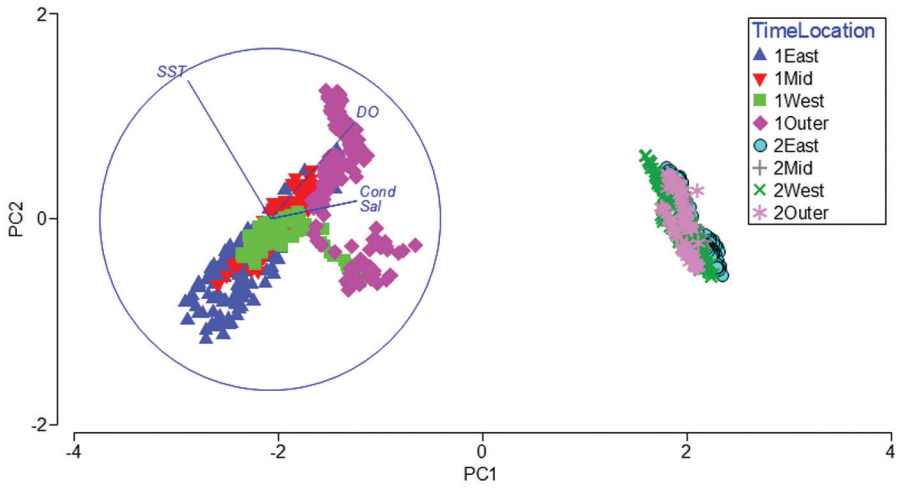

Fig. 7. Temporal variation in water quality parameters at El Escambrón a week and a month after tropical storm Isaías flooding event. This solution explains 98.5 % of the observed variation.

variation (Pseudo-F = 518.1, $p < 0.0001$), with a significant time x location interaction (Pseudo-F = 601.7, $p < 0.0001$). Conductivity increased from 36.3 to 54.4 mS cm^{-1} over the same period and showed similarly strong effects across factors (all $p < 0.0001$).

Dissolved oxygen rose from hypoxic levels (3.31 mg L^{-1}) after the storm to 8.56 mg L^{-1} one month later, with significant temporal (Pseudo-F = 13345, $p < 0.0001$), spatial (Pseudo-F = 228.3, $p < 0.0001$), and interaction effects (Pseudo-F = 293.5, $p < 0.0001$). SST remained relatively stable (30.04 → 29.44°C) but still showed significant spatio-temporal variation and interaction effects (all $p < 0.0001$). Together, these changes reflected rapid, storm-driven freshwater and hypoxic pulses followed by gradual short-term recovery. These results validate our first hypothesis suggesting that extreme rainfall and runoff led to significant coral mortality and regime shifts in coral reef benthic community structure, an effect not seen under previous hurricane and bleaching disturbances.

Case study 2 – Compounded mass coral bleaching effects on restored *Acropora palmata* at El Escambrón: The restored *A. palmata* population at El Escambrón showed 100 % survival during the first four months and 95 % after eight months (Fig. 8A). Despite the mass bleaching event of 2023, no meaningful mortality was documented. Survival declined to 88 % after 15 months, but the entire population collapsed following the 2024 compounded mass bleaching event. Spatio-temporal variation in survival was highly significant ($p < 0.0001$) with a significant time × plot interaction ($p = 0.0029$) (Table 4). Percent live tissue cover followed a similar pattern, remaining at 100 % after four months, 93 % after eight months, and 87 % after 15 months before collapsing in November 2024. Spatio-temporal variation was significant ($p < 0.0001$) with a significant interaction term ($p = 0.0040$) (Fig. 8B).

Colony surface area increased significantly from 83 to 231.46 cm^2 (1.8-fold) over 15 months (Fig. 8C), with strong spatio-temporal variation ($p < 0.0001$) and a significant time x plot interaction ($p = 0.0018$). Colony volume increased from 133.9 to 2288.2 cm^3 (1.6-fold) (Fig. 8D), with highly significant spatio-temporal variation and interactions ($p < 0.0001$). Colony height increased from 1.53 to 8.93 cm (4.8-fold) (Fig. 8E), again with significant spatio-temporal variation and interactions ($p < 0.0001$). Branch abundance rose from 0.15 to

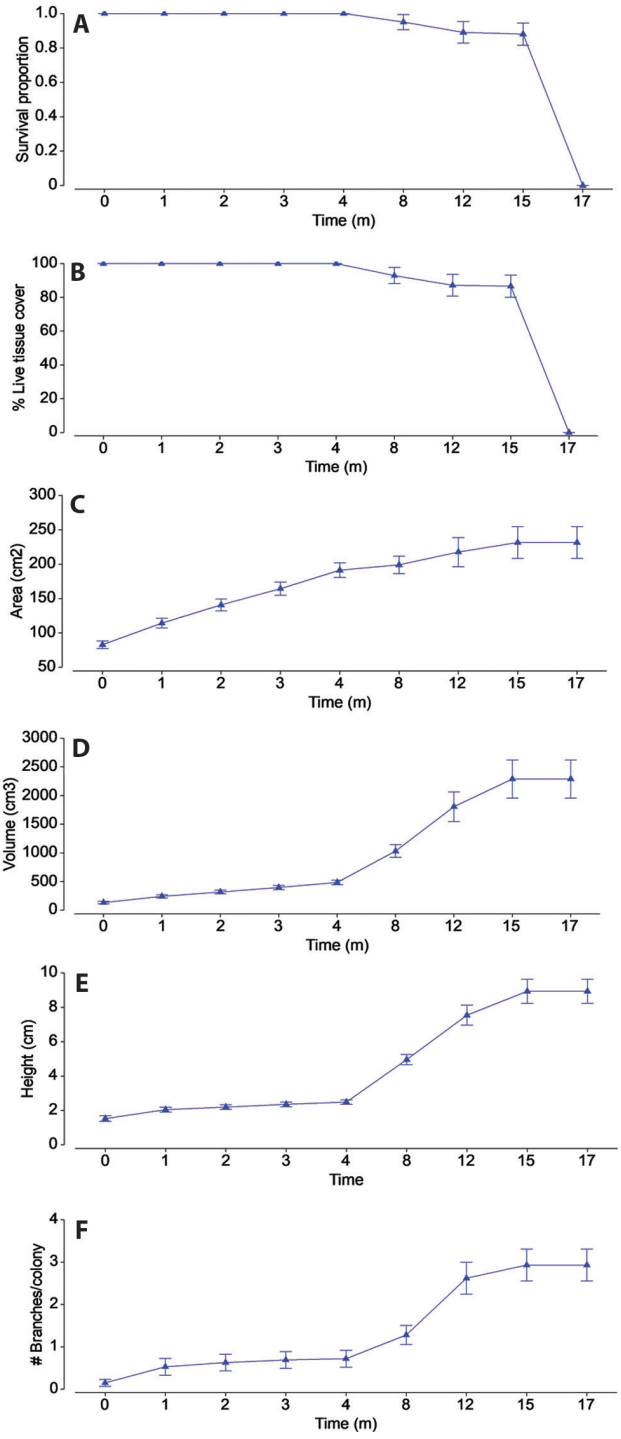

Fig. 8. Temporal variation in restored *Acropora palmata* demographic performance parameters at El Escambrón: **A.** Colony survival proportion, **B.** Percentage live tissue cover, **C.** Colony surface area (cm^2), **D.** Colony volume (cm^3), **E.** Colony height (cm), **F.** Branch abundance per colony. Mean ± standard error.

Table 4

Two-way permutational analysis of variance (PERMANOVA) results of spatio-temporal variation in restored *Acropora palmata* parameters at El Escambrón reef impacted by the 2023 and 2024 mass bleaching.

Source	df	Pseudo-F	P(perm)	Unique perms	√-Estimate of components of variation
Colony survival rate					
Time	8	412.28	< 0.0001	9 933	10.83
Plot	9	5.75	< 0.0001	9 934	1.23
Time x Plot	72	1.61	0.0029	9 829	1.32
% Live tissue cover					
Time	8	402.06	< 0.0001	9 946	27.06
Plot	9	5.73	< 0.0001	9 921	3.10
Time x Plot	72	1.57	0.0040	9 831	3.22
Colony surface area (cm^2)					
Time	8	70.46	< 0.0001	9 916	7.83
Plot	9	16.40	< 0.0001	9 937	3.89
Time x Plot	72	1.52	0.0018	9 834	2.15
Colony volume (cm^3)					
Time	8	207.31	< 0.0001	9 917	20.83
Plot	9	17.72	< 0.0001	9 921	6.25
Time x Plot	72	1.87	< 0.0001	9 806	4.27
Colony height (cm)					
Time	8	400.74	< 0.0001	9 931	16.00
Plot	9	21.27	< 0.0001	9 936	3.80
Time x Plot	72	2.14	< 0.0001	9 791	2.70
Colony branch abundance					
Time	8	66.45	< 0.0001	9 937	13.67
Plot	9	8.14	< 0.0001	9 922	4.76
Time x Plot	72	0.73	0.9619	9 839	-2.76

2.93 branches per colony (18.5-fold) (Fig. 8F), showing significant spatio-temporal variation ($p < 0.0001$) but no interaction effect (Table 4).

Some of the water quality parameters obtained through remote sensing showed important variations between 2023 and 2024 (Table 5). This was evidenced by the significant temporal variation observed in the multivariate environmental parameters' matrix between 2023 and 2024 ($p = 0.0077$) (Table 6). Easterly winds (wmd_ucmp) had a non-significant decline in annual average speed from -3.72 to -2.96 m s^{-1} between 2023 and 2024. Southerly winds (wmd_vcmp) had also a non-significant decline in annual average speed from 0.64 to 0.38 m s^{-1} between 2023 and 2024. This suggests dominance of doldrum conditions during 2024. However, doldrums magnified right before mass coral bleaching in both years. UGOS surface current vectors showed a non-significant decrease in westerly current speed from 0.07 to 0.04 m s^{-1} between 2023 and 2024, while the VGOS showed a non-significant increase in northerly surface currents shifting from -0.02 to -0.04 m s^{-1} between 2023 and 2024. These vectors suggest a predominantly westerly to northwesterly local component in the surface current direction during predominant doldrums, which brought abnormally warm waters from the marine heatwave located east and north of Puerto Rico.

Mean annual SST showed no significant change between years (29.3°C in 2023 vs. 29.0°C in 2024). However, SSTa increased

Table 5
Water quality parameters monthly means at El Escambrón reef impacted by the 2023 and 2024 mass bleaching.

Variable	0 (06/23)	1 (07/23)	2 (08/23)	3 (09/23)	4 (10/23)	8 (02/24)	12 (06/24)	15 (09/24)	17 (11/24)
wnd_ucmp (m s^{-1})	-4.19	-5.44	-4.44	-2.59	-1.92	-1.85	-3.78	-3.51	-2.69
wnd_vcmp (m s^{-1})	1.40	-0.04	0.58	0.39	0.85	-0.16	0.84	0.39	0.43
UGOS (m s^{-1})	0.10	0.14	0.03	0.09	0.01	0.03	0.06	0.04	0.03
VGOS (m s^{-1})	-0.23	-0.09	0.10	0.14	-0.01	0.02	-0.02	0.00	-0.16
SST (°C)	28.70	28.75	29.42	29.80	29.97	26.83	29.27	30.13	29.85
SSTa (°C)	0.55	0.28	0.26	1.18	0.58	0.99	1.83	1.67	1.75
HS (°C)	0.31	0.56	1.03	1.41	1.45	0.00	0.75	1.61	1.33
DHWs	0.00	0.00	1.41	5.98	12.43	0.01	0.25	6.44	18.66
Salinity (PSU)	36.28	37.45	36.11	36.92	37.81	34.03	34.26	33.96	NA
Kd490 (m^{-1})	0.07	0.04	0.05	0.06	0.04	0.07	0.05	0.07	0.11
PAR (einstein m^{-2} day^{-1})	51.04	47.02	47.37	46.33	39.01	39.53	38.47	48.06	NA
SPM (mg L^{-1})	0.15	0.19	0.21	0.28	0.31	0.45	0.67	0.44	0.66
Chl_a (mg m^{-3})	0.14	NA	0.36	0.25	0.21	0.72	0.98	0.80	0.62
PIC (mol m^{-3})	0.00001	NA	0.00017	0.00083	0.00012	0.00087	0.00013	0.00050	0.00132
POC (mg m^{-3})	79.50	47.80	66.36	76.36	49.66	121.07	58.35	95.93	166.61
NPP (mg C m^{-2} day^{-1})	579.67	405.75	414.09	472.60	333.31	765.88	374.81	591.15	976.74

*NA= Data not available for the sampling period.

Table 6
One-way permutational analysis of variance (PERMANOVA) results of annual variation in water quality parameters at El Escambrón reef impacted by the 2023 and 2024 mass bleaching.

Source*	Pseudo-F	P(perm)
Environmental matrix	2.96	0.0077
wnd_ucmp	0.87	0.3952
wnd_vcmp	0.67	0.6350
UGOS	1.48	0.2350
VGOS	0.07	0.7587
SST	0.20	0.1819
SSTa	15.29	0.0211
HS	0.005	0.9167
DHWs	0.26	0.6423
Salinity	57.38	0.0061
Kd490 (m^{-1})	4.31	0.0657
PAR (einstein m^{-2} day^{-1})	0.71	0.4002
SPM (mg L^{-1})	25.35	0.0081
Chl_a (mg m^{-3})	48.49	0.0068
PIC (mol m^{-3})	2.85	0.1282
POC (mg m^{-3})	4.78	0.0598
NPP (mg C m^{-2} day^{-1})	3.77	0.0933

*Degrees of freedom = 1,7.

markedly from +0.57°C to +1.56°C ($p = 0.0211$), highlighting the abnormal late summer SSTa during 2024 (Table 6). HS values showed no significant temporal difference (0.95 to 0.92°C) and mean annual DHWs rose non-significantly from 3.96 to 6.34. In contrast, maximum accumulated DHWs increased substantially—from 12.43 in 2023 to 18.66 in 2024—driving compounded mass bleaching events. DHW accumulation reached Alert Level 3 in 2023 and Alert Level 4 in 2024, thresholds largely exceeding severe coral bleaching and mortality (Fig. 9).

Mean annual salinity declined significantly from 36.9 ppt in 2023 to 34.1 ppt in 2024 ($p = 0.0061$), suggesting potential impacts from southeasterly mesoscale gyres (Table 6). Mean annual Kd_{490} increased slightly (0.05 to 0.07 m^{-1}), however, Kd_{490} increased to 0.11 m^{-1} by November 2024, coinciding with coral mortality, and exceeding the proposed water quality threshold for Puerto Rican coastal waters of 0.1 m^{-1} (Hernández et al., 2020; Torres-Pérez et al., 2026). PAR decreased (46.2 to 43.5 einstein

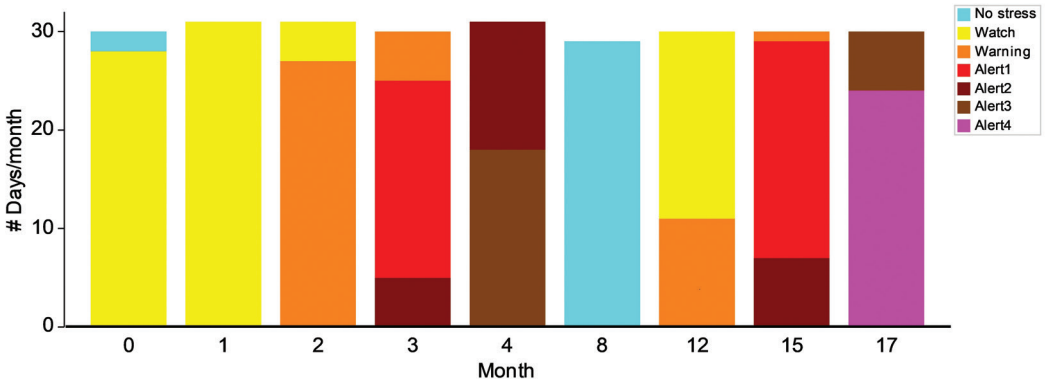

Fig. 9. Temporal variation in bleaching alerts during 2023 and 2024 at El Escambrón reef.

m^{-2} day^{-1}), both non-significantly. SPM rose significantly from 0.23 to 0.55 mg L^{-1} ($p = 0.0081$), even reaching levels of up to 0.67 mg L^{-1} between June and November 2024. Mean annual chlorophyll-*a* increased significantly from 0.23 to 0.78 mg m^{-3} ($p = 0.0068$), which largely exceeded the recommended coastal water quality threshold for Puerto Rico of 0.45 mg m^{-3} (Hernández et al., 2020; Torres-Pérez et al., 2026), and exceeding by up to 3.5-fold the conservative 0.2 mg m^{-3} eutrophication threshold (Mejías-Rivera et al., 2026). PIC showed a small, non-significant rise (0.0002 to 0.0007 mol m^{-3}), POC increased marginally (63.9 to 110.5 mg m^{-3}, $p = 0.0598$), and NPP showed a non-significant increase from 441.1 to 677.1 mg C m^{-2} day^{-1}.

Percentage survival of restored *A. palmata* at El Escambrón showed a significant multivariate correlation with the water-quality matrix (RELATE) (Rho = 0.622, $p = 0.0284$). BEST/BIOENV indicated that the strongest correlation (0.914, $p = 0.0470$) was explained by the combination of SSTa, bleaching alert level 4, chlorophyll-*a*, and POC. Percent live tissue cover showed an identical pattern (Rho = 0.622, $p = 0.0275$), with the same water quality variable group producing the highest correlation (0.914). These results validate our second hypothesis suggesting that compounded marine heatwaves, mass coral bleaching and declining water quality are strongly correlated to restored *A. palmata* mortality. It also highlights that exceeding recommended light attenuation and eutrophication thresholds can be a significant compounded factor under extreme heat conditions leading to coral mortality.

Case study 3 – Mass coral bleaching effects on restored *Acropora palmata* at Punta Melones: The restored *A. palmata* population previously dislodged by bottom swells from category five Hurricane Beryl in June 2024 at Punta Melones, Culebra, showed 100 % survival from August to October 2024 (Fig. 10A), followed by a highly significant decline to 2 % in November during the prolonged doldrum and the mass bleaching event ($p < 0.0001$), remaining at 1 % by January 2025 (Table 7). Survival showed significant spatial variation among plots ($p = 0.0488$) but no time × plot interaction. Percent live tissue cover was 94.7–95.9 % from August to October (Fig. 10B) but declined sharply to 1.3 % in November and to 0.7 % by February 2025 ($p < 0.0001$), with significant spatial variation ($p = 0.0006$) and no interaction effect.

Colony surface area showed a non-significant increase from 478 to 551 cm^2 prior to bleaching (Fig. 10C), with significant spatial variation ($p < 0.0001$) but no interaction. Colony volume increased significantly from 14.423 to 17.105 cm^3 ($p < 0.0001$) (Fig. 10D), with significant spatial variation ($p < 0.0001$)

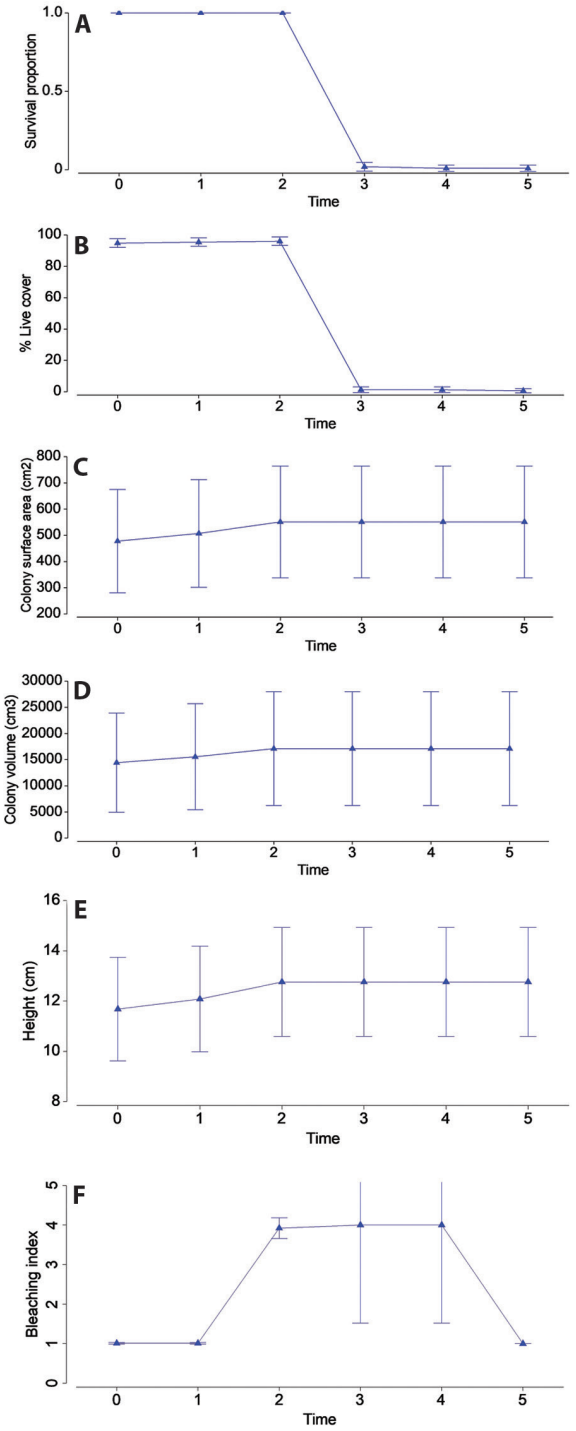

Fig. 10. Temporal variation in restored *Acropora palmata* demographic performance parameters at Punta Melones: **A.** Colony survival proportion, **B.** Percentage live tissue cover, **C.** Colony surface area (cm^2), **D.** Colony volume (cm^3), **E.** Colony height (cm), **F.** Bleaching index. Mean ± standard error.

Table 7
Two-way permutational analysis of variance (PERMANOVA) results of spatio-temporal variation in restored *Acropora palmata* parameters at El Escambrón reef impacted by the 2023 and 2024 mass bleaching.

Source	df	Pseudo-F	P(perm)	Unique perms	√-Estimate of components of variation
Colony survival rate					
Time	5	4 381	< 0.0001	9 941	18.01
Plot	9	1.78	0.0488	9 833	0.31
Time x Plot	45	0.78	0.9529	9 764	-0.41
% Live tissue cover					
Time	5	2 888	< 0.0001	9 940	45.50
Plot	9	3.10	0.0006	9 929	1.55
Time x Plot	45	0.65	0.6480	9 813	-1.55
Colony surface area (cm^2)					
Time	5	390.38	0.6793	9 928	-1.19
Plot	9	30.49	< 0.0001	9 912	16.17
Time x Plot	45	0.02	> 0.9999	9 837	-7.20
Colony volume (cm^3)					
Time	5	24.37	< 0.0001	9 924	12.43
Plot	9	49.46	< 0.0001	9 918	23.10
Time x Plot	45	0.01	>0.9999	9 962	-9.82
Colony height (cm)					
Time	5	0.66	0.6966	9 943	16.00
Plot	9	122.38	< 0.0001	9 935	3.80
Time x Plot	45	0.01	> 0.9999	9 874	2.70
Bleaching index					
Time	5	238.02	< 0.0001	9 974	4.27
Plot	9	3.14	0.0012	9 937	0.52
Time x Plot	45	2.64	< 0.0001	9 884	1.12

and no interaction. Colony height increased non-significantly from 11.7 to 12.8 cm (Fig. 10E), with significant spatial variation ($p < 0.0001$).

Mean bleaching index increased significantly ($p < 0.0001$) from 1.01 to 3.92 during bleaching before declining to 1.0, showing significant spatial variation ($p = 0.0012$) and a significant time × plot interaction ($p < 0.0001$) (Fig. 10F). SST increased significantly from 27.4°C in August 2024 to 30.4°C immediately before the mass bleaching and mortality event in October ($p < 0.0001$) (Table 8, Table 9). SSTa likewise intensified from +1.40 to +2.14°C ($p < 0.0001$), and HS values rose from 1.19 to 1.96°C ($p < 0.0001$). DHWs accumulated rapidly, increasing from 7.62 in August to 18.89 by November ($p < 0.0001$).

Table 8
Water quality parameters monthly means at Punta Melones reef impacted by the 2024 mass bleaching.

Variable	**0** (08/24)	**1** (09/24)	**2** (10/24)	**3** (11/24)	**4** (12/24)	**5** (01/25)
SST (°C)	29.63	30.19	30.40	29.35	28.41	27.41
SSTa (°C)	+1.40	+1.79	+2.14	+1.60	+1.54	+1.24
HS (°C)	1.19	1.75	1.96	0.90	0.14	0
DHWs	7.62	11.71	17.27	18.89	12.26	3.57

Table 9
One-way permutational analysis of variance (PERMANOVA) results of annual variation in water quality parameters at Punta Melones reef impacted by the 2024 mass bleaching.

Source*	Pseudo-F	P(perm)
Environmental matrix	230.5	< 0.0001
SST	638.5	< 0.0001
SSTa	121.4	< 0.0001
HS	560.9	< 0.0001
DHWs	146.3	< 0.0001

*Degrees of Freedom = 5,178.

Variation in restored *A. palmata* colony survival showed a significant multivariate correlation with the environmental matrix (Rho = 0.561, p = 0.0369), with BEST/BIOENV indicating that survival decline was primarily driven by increasing SST (correlation = 0.812, p = 0.0470). Percent live tissue cover showed a similar pattern, correlating significantly with the environmental matrix (Rho = 0.627, p = 0.0137), and BEST/BIOENV identified SST and HS as the strongest predictors (correlation = 0.747, p = 0.0110). These results validate our third hypothesis suggesting that compounded mass coral bleaching led to restored hurricane-dislodged *A. palmata* fragments mortality.

DISCUSSION

Case Study 1: The coral mortality event documented at El Escambrón in July 2020 represents a compelling example of how extreme rainfall and flood plumes from highly urbanized watersheds can induce stochastic declines in coral health, even in the absence of thermal stress, and major changes in community composition. *Acropora palmata* mortality increased significantly within one week after the extreme rainfall event, coinciding with a sharp drop in salinity (< 23 ppt), elevated turbidity, reduced dissolved oxygen concentration, and the advection of a dense sediment-laden, nutrient- and pollutant-loaded urban stormwater plume over the shallow reef terrace. Observations were consistent with documented Acroporid mortality elsewhere across adjacent reefs not part of this long-term study. These observations validate our first hypothesis suggesting that this acute rainfall and runoff event became the most significant driver of coral mortality in 17 years of long-term monitoring. No other previous mass bleaching, hurricane or winter swell disturbances led to significant coral mortality until tropical storm Isaías in 2020.

The observed mortality aligns with global evidence that acute salinity reductions of even 3–5 ppt can cause osmotic shock, tissue sloughing, and rapid necrosis (shutdown reaction) in Acroporids, especially when coupled with sediment deposition (Kerswell & Jones, 2003; Manzello, 2015). Storm-driven desalination and runoff has been implicated in mass mortality events across the Caribbean (Larsen & Webb, 2009; Kjerfve et al., 2021), Mozambique (Perry et al., 2003) and Thailand (Nakano et al., 2009), particularly in regions with degraded watershed infrastructure. The Escambrón event fits this pattern, highlighting the heightened vulnerability of *A. palmata* to urban freshwater toxicity, low-light stress from turbidity, prolonged anoxic conditions, and rapid shifts in pH and inorganic nutrient loads associated with combined sewer overflows.

Even otherwise stable coral colonies—many with > 85 % live tissue cover during at least 15 years prior to the event—suffered precipitous declines, with full or partial mortality occurring within days of plume exposure. The rapid onset of mortality suggests that the primary driver was a physiological collapse, rather than disease progression or chronic bleaching. This interpretation is supported by laboratory trials showing that Acroporid corals exhibit near-immediate polyp bailout or tissue loss under salinity < 28 ppt and high temperature (Chen et al., 2017; Inoue et al., 2012; True, 2012). Other coral species have also shown significant physiological stress and mortality under low salinity shock in combination with high temperature (Aguilar et al., 2019; Downs et al., 2009; Faxneld et al., 2010; Kerswell & Jones, 2003;

Kuanui et al., 2015). This event significantly exceeded that minimum threshold.

El Escambrón's position adjacent to heavily urbanized and flood-prone watersheds across the San Juan Bay estuary system—characterized by high impervious cover, inadequate stormwater management, and episodic sanitary overflows—likely exacerbated plume toxicity. Elevated levels of suspended sediments, fecal bacteria, heavy metals, and organic pollutants are common in Puerto Rico's coastal environments (Bachoon et al., 2010; Pait et al., 2008; Rodríguez-Sierra et al., 2019) and can synergistically intensify coral stress responses. There is unequivocal evidence of the chronic hypertrophic conditions of San Juan Bay estuary system (Ellis, 1976; Gómez-Gómez & Ellis, 1983; Pérez-Villalona et al., 2015; Webb & Gómez-Gómez, 1998). This combination of multiple pollutants displaced towards the reef by extreme runoff likely accelerated tissue mortality beyond what salinity alone would cause.

A particular concern of extreme runoff events during warm summer conditions as in this case is the potential combined impacts of deoxygenation and blooming and mixing toxic dinoflagellates and/or cyanobacteria in estuarine and coastal waters. A significant dry spell (~2–3 months) preceded tropical storm Isaías in 2020, characterized by reduced runoff and enhanced algal/cyanobacterial blooming on adjacent estuarine waters. These waters were flushed to coastal waters during the storm event. According to Bauza-Ortega et al. (2024), long-term water quality data (2018–2023) across numerous channels of the San Juan Bay estuary system that drain into coastal waters show mean chronic hypoxic conditions, including Caño Martín Peña (2.9 mg L^{-1}), Canal La Malaria (2.0 mg L^{-1}), Canal Blasina (1.1 mg L^{-1}), and Canal Suárez (3.4 mg L^{-1}). Also, lagoons and channels show unsustainable mean high turbidity, including Laguna de Piñones (17.4 NTU), Canal La Malaria (14.5 NTU), Laguna Los Corozos (12.4 NTU), and Laguna San José (12.1 NTU). Many of these systems also exhibit large fluctuations in water transparency, salinity, pH, oil and grease concentration, and nitrogen concentration, resulting from recurrent runoff pulse events. Studies conducted during the 2020 algal bloom just prior to tropical storm Isaías, showed that the planktonic community was dominated primarily by cyanobacteria *Microcystis wesenbergii* (Santos-Flores & Martínez-Rodríguez, 2024). Other toxic cyanobacteria such as *Anabaena*, *Planktothrix*, *Cylindrospermopsis*, *Dolichospermum*, and *Aphanizomenon* have been documented in dominant numbers in Laguna San José (Bauzá-Ortega et al., 2024; Santos-Flores & Martínez-Rodríguez, 2024).

Blooms of *M. wesenbergii*, a colonial cyanobacterium, pose significant ecological and public health risks in estuarine environments. These blooms can produce cyanotoxins (e.g., microcystins) (Cordeiro et al., 2020; Stoyneva-Gärtner et al., 2020; Tatters et al., 2021) that are harmful to aquatic organisms, leading to fish kills, reduced biodiversity, and disruption of food webs through oxygen depletion and shading of submerged vegetation. Dense surface accumulations limit light penetration, suppress primary producers such as seagrasses and benthic algae, and contribute to hypoxic or anoxic conditions during bloom decay. Hypertrophic conditions and high temperatures promote *Microcystis* blooming dynamics (Wu et al., 2014), while wind direction and speed may determine dispersion (Bonilla et al., 2026). Doldrum conditions were prevalent across the impacted zone during at least a week or so (Hernández-Delgado, personal observations, July 2020), therefore dispersion of blooming cyanobacteria was presumably slow. These findings highlight the hypothesis that cyanobacterial toxicity might have been one of the potential key drivers of *A. palmata* mortality documented in this study.

Certain cyanobacteria can form pathogenic microbial consortia that cause coral tissue lysis and death, leading to declines in coral reefs (Barott et al., 2011; Ford et al., 2018). They produce various secondary metabolites, some of which are toxic to reef organisms or inhibit coral recruitment (Charpy et al., 2012; Kuffner & Paul, 2004; Kuffner et al., 2006; Ritson-Williams et al., 2016; Ritson-Williams

et al., 2020; Vizon et al., 2024). Large runoff events often carry excess nutrients (nitrogen and phosphorus) into coastal waters (Fabricius et al., 2005; Vega Thurber et al., 2014). This nutrient enrichment can fuel the growth of cyanobacteria, leading to harmful algal blooms (HABs) that outcompete corals for space and resources, reduce light availability, and create hypoxic or anoxic conditions, further stressing coral reef ecosystems (Fabricius et al., 2005; Lapointe et al., 2004). Runoff also carries sediments that increase turbidity, reducing light penetration, which is essential for the symbiotic algae (zooxanthellae) within coral tissues to photosynthesize (Fabricius et al., 2005; Vega Thurber et al., 2014). Settling of excess sediments can directly smother coral polyps, hindering their ability to feed and respire (Erftemeijer et al., 2012; Fabricius et al., 2005). These combined effects can potentially lead to strong acute ecophysiological effects on corals that might lead to mortality. Reefs dominated by benthic cyanobacterial mats produce significantly fewer ecosystem services associated with healthy coral-dominated reefs, including long-term reduced coastal protection and declining herbivory (Ford et al., 2017; Ford et al., 2021).

These compounded conditions could exacerbate synergic impacts on corals under projected warming trends and stronger, prolonged marine heatwaves (Hernández-Delgado & Rodríguez-González, 2025). Stressed corals are more susceptible to diseases (Fabricius et al., 2005; Vega Thurber et al., 2014), and to warming (Manzello et al., 2025), further accelerating their decline. These compounded impacts highlight the severe threat that mixed runoff events pose to coral reefs under abnormal warming, underscoring the need for effective management strategies to reduce land-based pollution and protect these valuable ecosystems (Hughes et al., 2017).

Importantly, long-term monitoring in this study shows that the 2020 storm-driven flood event triggered a stepwise shift in benthic community structure and in *A. palmata* population trajectory, after which live tissue cover remained depressed, colony fragmentation increased, and susceptibility to subsequent heat stress events in 2023 and 2024 became more pronounced. Similar long-term post-plume degradation has been observed in Florida and Jamaica, where recurring freshwater pulses reduce coral resilience to subsequent stressors (Toth et al., 2019). Observed lack of recovery contrast rapid recovery rates documented in Pacific coral reefs following mass bleaching events (Huntington et al., 2022).

Furthermore, to interpret the results, we relied on the proposed water quality thresholds for coastal waters in Puerto Rico of 0.1 m for Kd_{490} and of 0.45 mg/m^{-3} for chlorophyll-*a* concentration (Hernández et al., 2020; Torres-Pérez et al., 2026). We also relied on the conservative 0.2 mg/m^{-3} eutrophication threshold. Results stress out that water quality pulse events, in possible combination with mesoscale oceanographic factors, might have affected water quality, leading to a strong association between water quality decline and coral mortality.

Collectively, Case Study 1 demonstrates that extreme urban flood pulses have emerged during the Anthropocene as a major acute driver of benthic community phase shifts on shallow urban coral reefs and a critical driver of mortality in Caribbean Acroporids, with increasing compounded effects of marine heatwaves, bleaching, hurricanes, and disease. For urban coastal coral populations such as El Escambrón, watershed restoration and stormwater runoff control are therefore not optional—they are foundational to long-term coral conservation and recovery.

Case Study 2 – The 2023–2024 compounded bleaching and water quality impacts on restored *Acropora palmata* at El Escambrón: The back-to-back mass bleaching events of 2023 and 2024 at El Escambrón demonstrated the cumulative nature of compounded thermal stress and declining water quality on restored *A. palmata* resilience. Before bleaching onset in 2023, restored colonies had 100 % survival rate, high live tissue cover (≈95 %), increasing surface area, and growing colony volume, indicating strong performance under shallow urban

reef conditions. Survival rate was 95 % after the 2023 event. However, within less than six months, abnormal SSTa affected corals again in 2024. Once the heatwave strengthened and bleaching affected corals again, live tissue cover fell from near-complete health to < 1 % within less than one month, with statistically significant losses across all metrics ($p < 0.0001$).

This collapse aligns with emerging literature showing increasing recurrence of mass bleaching events (Destri et al., 2025) and highlighting that consecutive, compounded heatwaves prevent coral physiological recovery, produce symbiont shifts with maladaptive outcomes, and reduce host energetic reserves (Baker et al., 2018; Morikawa & Palumbi, 2019). Colonies at El Escambrón likely entered the 2024 heatwave still energetically depleted from the 2023 event, leaving insufficient reserves for shuffling or switching of symbiont communities (Stat et al., 2013). This "carryover bleaching susceptibility" phenomenon has become increasingly common across the Caribbean and Pacific following compounded bleaching effects.

Crucially, El Escambrón is also a highly urbanized and chronically stressed shallow coastal reef site, with documented impacts of poor optical water quality, chronic sedimentation, high turbidity, and reduced dissolved oxygen and optical brighteners concentration on coral recruitment (González-Figueroa & Hernández-Delgado, 2021). These background stressors can reduce maximum photosynthetic rates (Anthony & Hoegh-Guldberg, 2003), suppress heterotrophic compensation mechanisms, and exacerbate bleaching mortality risk (Cunning & Baker, 2013). The interaction of chronic stress and successive bleaching events likely explains the near-total mortality observed across restored colonies. Furthermore, the strong association of warmer conditions and declining water quality with restored coral collapse strongly supports the hypothesis that compounded bleaching and water quality decline affects *A. palmata* populations.

Case Study 3 – The 2024 thermal bleaching event impacts on restored *Acropora palmata* at Punta Melones, Culebra: The 2024 marine heatwave at Punta Melones produced one of the most rapid and severe *A. palmata* mortality episodes ever documented. Prior to the heatwave, post-hurricane Beryl coral restoration was a success, despite abnormally high SST. Colony survival at this site was 100 %. However, within four weeks of exposure to prolonged temperatures >30.4 °C (though SST within shallow backreef habitats reached ~32–34°C during several weeks), survival plummeted to 2 %, representing near-total collapse of the population. This event represents another example of a carryover bleaching susceptibility phenomenon affecting still energetically depleted coral colonies from the 2023 mass bleaching event, leaving insufficient reserves for shuffling or switching of symbiont communities (Stat et al., 2013). Acroporids are highly susceptible to rapidly dispersing diseases (Mercado-Molina et al., 2020; Sutherland et al., 2011; Williams & Miller, 2005). However, this mortality trajectory parallels the extreme Acroporid losses observed during the 2005 Caribbean-wide bleaching event (Eakin et al., 2010; Wilkinson & Souter, 2008), as well as extreme bleaching-related mortality in the Pacific (Vargas-Angel et al., 2019), yet the rate and extent of the 2024 collapse may indicate that climate-driven thermal stress has reached a new threshold of severity relative to past decades as projected by Hernández-Delgado & Rodríguez-González (2025).

Repeated thermal bleaching undermines Acroporid fitness by disrupting host–symbiont relationships, reducing photosynthate supply, and inducing reactive oxygen species (ROS) accumulation (Cziesielski et al., 2019; Weis, 2008). *Acropora palmata* is considered moderately heat-sensitive compared to other branching corals and can be significantly sensitive to recurrent bleaching stress as found in other corals (Grottoli et al., 2014), but our results reveal mortality far exceeding typical bleaching-associated

declines. This suggests that the co-occurrence of sub-lethal thermal physiological stress and pre-existing environmental degradation—including earlier bleaching in 2023, chronic nutrient enrichment, reduced herbivory, and recent strong hurricane-generated bottom swell impacts—likely weakened Punta Melones corals prior to the 2024 heatwave. This is consistent with previous studies suggesting corals under recurrent bleaching events are physiologically compromised and have limited recovery ability (Baumann et al., 2014).

Reefs in Culebra Island including Punta Melones and adjacent locations have been chronically affected by sediment loads (Gómez-Andújar & Hernández-Delgado, 2020; Otaño-Cruz et al., 2017; Otaño-Cruz et al., 2019; Ramos-Scharrón et al., 2012), sewage pulses (Hernández-Delgado et al., 2017), and eutrophication (Hernández-Delgado & Ortiz-Flores, 2022). Also, recent strong hurricanes disrupted *A. palmata* populations across eastern Puerto Rico (Hernández-Delgado et al., 2024). There is a growing concern that increasing SST and ocean heat content can lead to stronger hurricanes under projected warming trends (Mann, 2024; Méndez-Tejeda & Hernández-Ayala, 2023; Murakami et al., 2018). This could result in a wider dispersion of mechanical impacts, including significant colony fragmentation, colony dislodgment, and physical destruction of reef frameworks even at long distances (>100–300 km) such as in the case of the hurricane-impacted Punta Melones restored *A. palmata* population.

The speed of population collapse further implies that colonies exceeded their thermal tolerance thresholds, unable to recover photochemical efficiency at night or during cooler intervals—a pattern consistent with acute heatwave mortality systems described in Guam and the Great Barrier Reef (Hughes et al., 2017; Schoepf et al., 2015). This case underscores that *A. palmata* populations with low physiological redundancy and limited thermal refugia may experience irreversible decline under modern heatwave regimes.

Recurrent marine heatwaves have become one of the primary drivers of global coral decline, pushing many reefs past their ecological thresholds. Successive thermal stress events reduce corals' bleaching tolerance and shorten recovery windows, leading to the carryover bleaching susceptibility phenomenon and to increasingly severe bleaching and mortality (Hughes et al., 2017; Hughes et al., 2018). Repeated heat exposure depletes coral energy reserves, disrupts photosynthesis, impairs calcification, and weakens immunity, leaving colonies physiologically exhausted and less capable of surviving subsequent extreme heat events (Bessell-Browne et al., 2021; Grottoli et al., 2006; Grottoli et al., 2014; Schoepf et al., 2015) or other types of disturbances. As recovery intervals shrink from decades to just a few years, or even months such as this case, many species—particularly reef-building *Acropora* spp.—are unable to rebuild lipid stores, regenerate lost tissue, or regain reproductive output before the next heatwave strikes (Baird & Marshall, 2002; Briggs et al., 2024; Johnston et al., 2020; Leggat et al., 2019). These cumulative stresses drive widespread shifts from coral- to algal-dominated communities, reducing structural complexity, altering fish assemblages, and diminishing overall ecosystem functioning and resilience (Graham et al., 2015; Mumby et al., 2007; Smith et al., 2006; Stuart-Smith et al., 2018). Moreover, marine heatwaves interact synergistically with pollution, sedimentation, eutrophication, and disease, amplifying coral vulnerability and accelerating population collapse (Manzello et al., 2025; Randall & van Woesik, 2015; Randall & van Woesik, 2017; Vega Thurber et al., 2014). Together, these studies demonstrate that recurrent marine heatwaves are not isolated disturbances but a chronic, escalating threat that is transforming coral reef ecosystems worldwide, and that are projected to enhance threats to coral reef conservation and restoration outcomes across the wider Caribbean under projected warming trends (Hernández-Delgado & Rodríguez-González, 2025).

Together, the three case studies provide a comprehensive window into the multi-driver

collapse of *A. palmata* in Puerto Rico's nearshore environments. Despite differing primary stressors—urban flood pulse (Case 1), consecutive bleaching with chronic stress (Case 2), and the 2024 unprecedented heatwave (Case 3), —all sites exhibited catastrophic tissue loss, consistent with increased marine heatwave frequency and severity (Rodrigues et al., 2025), accumulated heat stress and bleaching (Skirving et al., 2019), and with the region-wide decline of Acroporids in the Anthropocene (Bon et al., 2026; Estrada-Saldívar et al., 2019; Rodríguez-Martínez et al., 2014). These events have led *A. palmata* to an enhanced risk of functional extinction due to severe permanent Allee effects. The wild *A. palmata* population at El Escambrón was estimated to exceed 5 000 colonies in 2016 (Hernández-Delgado, unpublished data). Only five surviving colonies were documented after the 2020 runoff event, suggesting a 99.9 % loss. Also, 100 % of the 500 out-planted corals at El Escambrón collapsed after the 2024 compounded mass bleaching event and declining water quality. Meanwhile, from a total of ~3 500 *A. palmata* out-plants at Punta Melones only seven colonies survived the 2024 mass bleaching event, representing a 99.8 % loss. Under such conditions, the physical isolation and decimated state of remnant colony survivors is a paramount obstacle for successful reproduction, which in turn leads to functional extinction, at least at the scales of our study locations.

Several key patterns emerge from our findings. First, *A. palmata* mortality is now driven by the interplay of acute and chronic stressors. While historically dominated by disease outbreaks and hurricanes (Aronson & Precht, 2001; Williams & Miller, 2006), modern mortality appears heavily associated with compound chronic events, where prolonged thermal stress, freshwater toxicity, turbidity pulses, and nutrient enrichment interact synergistically (Donovan et al., 2020, Donovan et al., 2021; Hughes et al., 2017). This has led to unprecedented mortality rates and population collapse, resulting in functional extinction of foundational reef-building species such as *A. palmata* (Manzello et al., 2025). Legacy effects and disturbance memory seem to play also a vital role in understanding ecosystem responses to disturbance regimes (González-Barrios et al., 2023).

Secondly, shallow urban reefs show dramatically reduced resilience under present warming trends. Sites such as El Escambrón and Punta Melones suffer not only from heatwaves but also from optical degradation, pollution, and altered hydrology, resulting in lower thermal thresholds and heightened bleaching severity. Ecological recovery windows no longer exist. The recurrence of disturbances within months prevents corals from accumulating energetic reserves, recovering symbiont densities, or regrowing lost tissue, driving progressive decline (Sully et al., 2019; Sully et al., 2022) or acute population collapses due to severe shutdown reactions. Also, rapid pre-mortality growth does not confer resilience. Despite positive *A. palmata* growth trajectories before the bleaching events, colonies collapsed rapidly once exposed to water quality decline and extreme heat, suggesting that physiological performance under stable seasonal conditions does not predict tolerance to extreme thermal or runoff events. Furthermore, *A. palmata*, already functionally extinct in many regions, is now entering a regime of near-zero natural persistence without intervention. The mortality documented across the three case studies matches the pattern of functional extinction described for Acroporids across the Caribbean (Manzello et al., 2025) and deserves further recognition and study.

The three cases examined in this study collectively demonstrate that *A. palmata* populations in Puerto Rico now exist in an ecological regime defined by acute disturbance sensitivity and chronic environmental degradation. Across all sites—El Escambrón and Punta Melones—colonies experienced catastrophic mortality (98–100 %) in response to recurrent extreme thermal events, low-salinity urban runoff pulses, and compounding bleaching. These findings reveal that *A. palmata*, once the dominant reef-building coral of Puerto Rico's shallow

reefs, is now unable to withstand the frequency, magnitude, and combination of contemporary climate and water-quality stressors.

Case Study 1 showed that even short-lived freshwater pulses from extreme rainfall can trigger immediate mortality, especially in urban coastal reefs adjacent to large human population centers. Case Study 2 confirmed that consecutive bleaching events, layered on a background of chronic pollution and declining optical water quality, result in near-total collapse of even previously healthy restored colonies. Case Study 3 demonstrated that acute marine heatwaves alone can eliminate entire restored populations within weeks, highlighting the need to identify and targe thermal refuge habitats as a future alternate restoration strategy. Together, these results provide unambiguous evidence that the natural persistence of *A. palmata* in Puerto Rico is no longer viable without targeted intervention and careful science-based selection of restoration sites.

The broader pattern across the three case studies aligns with Caribbean-wide evidence that the species is entering a potential state of functional extinction, with recruitment failure, low genetic diversity, and ecosystem fragmentation undermining long-term survival, which deserve further study. The losses documented here could have profound implications not only for coral conservation but also for coastal protection, because *A. palmata* is a foundational species that historically reduced wave energy and stabilized nearshore habitats. This leads to critical recommendations for implementing conservation and restoration interventions.

There is a vital need to implement proactive restoration to prevent local extirpation. Given the near-total mortality observed at all study sites, immediate intervention is required to preserve genetic diversity and prevent irreversible local extinction. Efforts should prioritize in situ nursery propagation and ex situ safeguarding of surviving genotypes, assisted gene flow between different locations in Puerto Rico, Culebra, Vieques, and other Caribbean Acroporid stocks, and rapid deployment of out-planting modules in suitable high-water-quality refugia – reefs subjected to strong currents, cooler temperatures, high dissolved oxygen concentration and planktonic supply that can boost coral survival and growth. This is highly consistent with modeled environmental predictors for restoring *A. palmata* (Banister et al., 2024).

It would also be important to establish thermal refugia for coral reintroduction. Future restoration must strategically select sites with higher flushing rates, greater thermal variability (which can enhance acclimatization), minimal urban runoff exposure, stable optical conditions – marginal urban reefs adjacent to river outlets, sewers or other runoff sources should be avoided unless watershed improvements are implemented. Addressing chronic land-based pollution as a prerequisite for restoration is also fundamental. The strong influence of salinity drops, turbidity, chlorophyll-*a* anomalies, and particulate loads indicates that stormwater infrastructure must be modernized, combined sewer outflows must be mitigated, and sedimentation and nutrient inputs must be reduced at the watershed scale. Without these improvements, restoration efforts might fail to produce long-term survivorship.

There is also a need to integrate predictive climate modeling into restoration planning (Hernández-Delgado & Rodríguez-González, 2025). Given the recurrence of heatwaves, downscaled climate projections should inform restoration timing. Coral plantings should avoid late-summer peak heating windows. Restoration programs should incorporate thermal stress early-warning systems (e.g., NOAA's Coral Reef Watch Program virtual buoys systems). Expanding thermal tolerance and stress-hardening research has also become crucial. The collapse of even rapidly growing colonies indicates the need for preconditioning experiments to increase thermal tolerance, symbiont manipulation (e.g., *Durusdinium* spp. associations), genetic screening for heat-tolerant strains, and the integration of shading strategies on *in situ* nurseries and restored populations.

Building multi-species, functionally diverse reef assemblages has become increasingly important. To enhance wave attenuation and

ecological resilience there is a mounting need to combine *A. palmata* with *Orbicella*, *Pseudodiploria*, branching *Porites* spp., and other species to enhance functional diversity. It is also important to integrate structural enhancement modules to increase rugosity through integrated green-gray restoration (Hernández-Delgado, 2024) and novel inter-disciplinary approaches (Viehman et al., 2023), and promoting reef fish recovery to restore grazing pressure and promote nutrient hotspots to foster enhanced demographic performance of restored corals (Hernández-Delgado & Laureano, 2024; Hernández-Delgado et al., 2025; Huntington et al., 2017). In addition, strengthening long-term monitoring for early detection of decline is central. Monitor vital parameters such as coral health and demographic performance, symbiont densities, optical water quality, water chemistry, and thermal anomalies.

Establishing high-resolution baselines allows early warning before mass-mortality episodes. Further, it could allow to identify vital windows of time to implement emergent measures such as shading or probably coral nursery relocation to deeper waters to minimize bleaching impacts. However, using natural thermal refugia as the backbone of the strategy is paramount for *A. palmata* population recovery.

Thermal Refugia–Centered Restoration Strategy for *Acropora palmata*: A refugia-based coral restoration framework is vital for the recovery of functionally extinct *A. palmata* (Fig. 11).

It could start by mapping and validating true thermal refugia. Not every cooler site is a real refugium. For *A. palmata*, there is a need to use high-resolution temperature loggers (HOBOs, etc.) across candidate reefs for at least 1–2 summers. This can allow looking for lower maximum temps, shorter duration above 30.5–31°C, or strong diel variability (upwelling, internal waves, mixing). It could be combined with good optical water quality (low turbidity, lower chlorophyll-*a*, low CDOM) and with limited land-based pollution (no direct river plumes, urban drainage, or marinas right on top). Another strategy should include overlaying with any existing survivor or "hold-out" colonies of *A. palmata* that made it through recent heatwaves — those sites are prime candidates. Any "core" restoration and broodstock nurseries for *A. palmata* should be located within or immediately adjacent to these thermally and optically buffered areas, not at chronically hot, turbid, urban sites, unless watershed conditions are drastically improved.

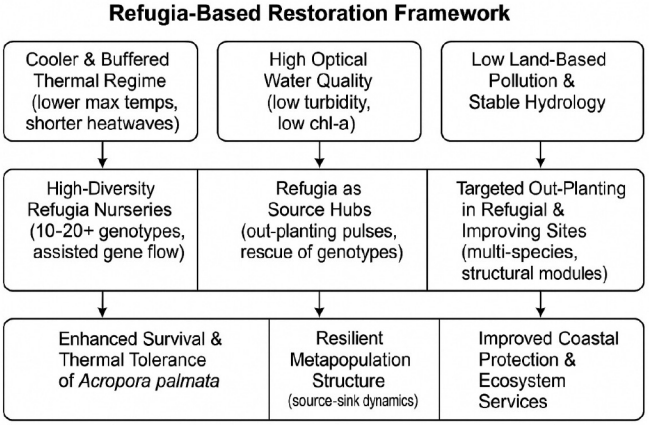

Fig. 11. Refugia-based coral restoration framework centered at the recovery of functionally extinct *Acropora palmata*.

Refugia should be used as source hubs for regional metapopulations. Thinking of thermal refugia as natural coral nurseries (*sensu* Hernández-Delgado & Laureano, 2024) and as genetic and demographic engines maintain high-diversity nurseries (many genotypes per site) in refugia. These will allow supplying out-plants to more marginal reefs in "pulse" restoration efforts when conditions are favorable (cooler years, La Niña, etc.) and using them to rescue and bank genotypes from reefs that are about to crash. High-rugosity, lower-energy forereefs and spur-and-groove zones that still get good flushing but have some depth buffer (e.g., 3–8 m instead of shallow 1–2 m bathymetry that gets extremely hot in heatwaves) should be prioritized. Refugia become permanent, high-protection seed banks and should never be fully mined; branches/fragments should be strategically harvested to repopulate other sites.

It would also be important to match genotypes to refugia and carry out assisted gene flow smartly. For severely depleted *A. palmata* population recovery, refugia can be used to concentrate thermally tolerant genotypes (survivors of recent events) and to integrate cross-location and cross-island stocks in controlled mixes. Where possible, nursery propagation (clippings) should be combined with sexual recruitment support (gamete collection, larval rearing, settlement on conditioned substrates) and placing recruits back into refugia. It would also be important to keep genotypes tracked and mixed intentionally, and to avoid creating monoculture reefs that may all share the same vulnerability. Designing each refugium nursery with 10–20+ distinct genotypes if available would also be crucial. Thermal refugia are not just cooler places — they are active hubs for maintaining and reshuffling genetic diversity, providing raw material for future adaptation.

Adjusting restoration expectations and strategy for non-refugial sites would be paramount. Heavily impacted and/or depleted sites should be treated as demonstration/socio-ecological sites, not as primary conservation reservoirs. Robust structure-focused green-grey designs (3D modules, wave-attenuation structures) should be used with mixed coral assemblages under some critically degraded coastal conditions (Hernández-Delgado, 2024), where *A. palmata* is a component but not the only pillar. It should also be combined with strong community engagement and education. However, *A. palmata* should be out-planted only if there is at least some evidence of reduced local stress (improved stormwater management, less sewage, better water transparency), if refugium-derived genotypes are used and are willing to accept that losses might be higher and more frequent, and if refugia sites are used to protect the species, and high-profile, marginal reefs are used to protect social value and awareness, but you do not expect the same ecological performance from both.

Monitoring and feedback rules should be tailored to refugia. For a refugium-based restoration program, it is vital to define clear triggers. First, if a refugium's temperatures start resembling non-refugial sites (e.g., repeated days >31–31.5 °C, or more frequent heat spikes), downgrade its role from source to priority site for protection / shading / active cooling trials. Secondly, there is a need to use rapid response protocols, including temporary shading during peak heatwaves (experimental but promising in small scales), enhanced disease monitoring and treatment response immediately post-stress. It should also include extra nutrient/sediment controls if there are local land-based inputs. Refugia sites are not "set and forget." They require very high monitoring intensity, because they anchor the entire long-term restoration strategy.

Increasing marine heatwaves and climate-driven extreme events are increasingly threatening coral reef conservation and restoration outcomes across the wider Caribbean and eastern tropical Pacific. However, they represent fundamental opportunities for modifying and adapting restoration strategies vital for recovering rapidly declining coral species that are potentially reaching functional extinction and fully depend on novel restoration strategies.

Author contribution statement: E.A. Hernández-Delgado was responsible for the conception and design of the study, for resource allocation, coral out-planting, long-term monitoring and coral restoration design and intervention, data collection coordination, data processing, statistical analysis and interpretation of results, and preparation of the manuscript. A.N. Ramos-Rosado was responsible for the conception and design of the study, data collection, data processing, statistical analysis and interpretation of results, and preparation of the manuscript. J.S. Fonseca-Miranda, R. Laureano, S.A. Hernández-Rodríguez, and A. Birriel-Ramos were responsible for coral restoration intervention and data collection. S.E. Suleimán-Ramos was responsible for the conception and design of the study, for resource allocation, for permitting procedures, field logistics coordination, coral out-planting, and data collection.

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