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Response of Caribbean coral reef assemblages to a category 5 Hurricane

Cassandra de Alba-Guzmán[1] · Alma Paola Rodríguez-Troncoso[1] · María del Carmen García-Rivas[2] · Fabián A. Rodríguez-Zaragoza[3]

Received: 30 June 2025 / Accepted: 13 November 2025
Published online: 24 November 2025

Abstract

Chinchorro Bank is the largest atoll reef in the northern Mesoamerican Reef, and due to the location, the coral assemblage is highly vulnerable to storms and hurricanes. In the context of climate change, with more intense hurricanes, it is highly relevant to analyze the damage and response of the hermatypic coral assemblage after these events. Three sites (La Caldera, La Baliza, and Chancay) at two zones [shallow (≤ 12 m) and deep (> 12 m)] were surveyed before and after the passage of Hurricane Dean (Category 5, Saffir–Simpson scale) in 2007. The results indicated that deeper zones recorded higher sponge (4.8%) and macroalgae (26.3%) coverage, and topographic complexity ($C = 0.27$), while the shallower zones harboured the highest live coral coverage. Hurricane Dean modified the structure of the coral assemblage with a loss of species and richness of morpho-functional groups and a reduction in the live coral cover, with differences among sites and zones. La Baliza recorded the highest losses in live coral cover (43.3%), species richness (48.7%), and diversity (37.5%), with no apparent recovery. Shallower reef zones were more negatively affected than deeper areas, showing an average loss of 24.3% live coral coverage following the disturbance. These results suggest that coral reefs have different susceptibilities to tropical cyclones in the same region and across depths, which, in both the short and long term, will shape the assemblage and persistence of Chinchorro Bank coral reefs.

Keywords Coral reef · Hurricane · Mesoamerican reef · Coral coverage · Caribbean Sea

1 Introduction

Hermatypic corals are the main framework builders of coral reef ecosystems with the capacity to calcify and form three-dimensional structures that contribute to the spatial heterogeneity and topography of the reef [1, 2]. These structures maintain a high biodiversity by providing habitat, food, and shelter, influencing the organism's abundance and ecological

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s44289-025-00105-1.

✉ Alma Paola Rodríguez-Troncoso, alma.rtroncoso@academicos.udg.mx; ✉ Fabián A. Rodríguez-Zaragoza, fabian.rzaragoza@academicos.udg.mx; Cassandra de Alba-Guzmán, cassandra.ag.bio@gmail.com; María del Carmen García-Rivas, mcgarcia@conanp.gob.mx | [1]Laboratorio de Ecología Marina, Centro de Investigaciones Costeras, Centro Universitario de La Costa, Universidad de Guadalajara, Avenida Universidad de Guadalajara No. 203, Puerto, Vallarta 48280, Jalisco, México. [2]Dirección General de Conservación, Comisión Nacional de Áreas Naturales Protegidas (CONANP), Av. Ejército Nacional No. 223, Col. Anáhuac I Sección, Alcaldía Miguel Hidalgo, Ciudad de México 11320, México. [3]Laboratorio de Ecología, Conservación y Taxonomía (LEMITAX), Departamento de Ecología Aplicada, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Camino Ramón Padilla Sánchez No. 2100, Nextipac, Zapopan 45200, Jalisco, México.

diversity [3, 4]. The benefits corals provide may change in response to their assemblage [1, 5]; therefore, the richness of associated species will respond to the species diversity and the morpho-functional groups, where branching and submassive corals are known as the major contributors to the complexity of the habitat availability [6]. Additionally, a high diversity of coral species may contribute to the genetic diversity and physiological thresholds that allow the individuals to respond to adverse conditions, decreasing the community vulnerability and possible ecological collapse after disturbances [7].

As in the rest of the world, the coral reefs in the Mexican Caribbean have suffered a drastic decline in coverage of more than 50% [8, 9]. Likewise, a shift in species dominance has been observed, with a replacement of branching and submassive corals such as *Acropora* spp. and *Orbicella* spp. by weedy corals, such as *Porites astreoides*, *Agaricia* spp., and *Siderastrea* spp. that develop less structural complexity [10–12]. The magnitude of this transformation in reef structure and composition results from the synergic effect of natural and anthropogenic pressures [13]. Among the main environmental drivers are the rising sea surface temperature, which induces coral bleaching events, coastal eutrophication from agricultural and urban runoff, overfishing, which alters food webs and diminishes key populations such as herbivorous fish, and diseases that cause the loss of coral tissue [12–16]. However, another increasingly alarming factor is tropical storms and hurricanes, which have become more intense in the last three decades [17, 18].

Hurricanes act as a stressor for coral reefs, primarily by causing direct physical damage to coral colonies through strong hydrodynamic forces and sediment resuspension [19]. In addition, they increase terrestrial runoff, which transports sediment, nutrients, and bacteria into the marine environment [20]. These sediment inputs reduce light penetration in the water column and can smother the coral tissue, initially impairing photosynthesis and eventually threatening coral survival [19, 21]. Additionally, increased nutrients favor the proliferation of macroalgae [22], reducing the availability of substrata for coral recruitment and growth, which also affects the photosynthetic efficiency of their symbionts (*Symbiodinium*) by blocking light [23]. Also, it is worth noting that macroalgae show greater resistance to hurricanes due to their rhizoidal system and compact morphology, which allows them to withstand intense waves and survive sedimentary abrasion in high-energy areas [24]. Moreover, they are fast colonizers and can rapidly occupy the available space left by dead corals [4]. As a result, there is a decrease in coral coverage following tropical cyclones, accompanied by a phase shift towards macroalgae dominance, affecting the reef's ecological balance and net calcification [12, 25].

Of particular concern is the impact that extreme events, such as hurricanes, can have on reefs of great ecological and socioeconomic relevance, such as Chinchorro Bank. This is Mexico's largest and most important coral reef, with a record of 1,030 species, 58% of which are marine species [26]. It is a Natural Protected Area (NPA) where regulated, small-scale, artisanal fishing focused on the pink snail (*Lobatus gigas*), spiny lobster (*Panulirus argus*), and other species of fish (e.g., *Serranidae, Lutjanidae, Haemulidae*) is permitted [18, 27]. The management plan also supports tourism activities regulated by a carrying capacity, which also economically benefits the coastal communities in the southern Mexican Caribbean [28]. Finally, Chinchorro Bank Biosphere Reserve is an important coral reef conservation area as it harbors ≈150 fish species and ≥ 90 species of hard and soft corals, including the branching species *Acropora palmata* and *Acropora cervicornis*, both listed under special protection in the Mexican Official Norm NOM-059-ECOL-2001, and international listings such as the Red and CITES list [29]. Considering its ecological and economic significance, it is essential to understand the spatio-temporal variation of the hermatypic coral assemblage, both at taxonomic and morpho-functional levels, in three sites of Chinchorro Bank after the passage of Hurricane Dean (a category five hurricane Saffir–Simpson scale), which directly impacted the region. The long-term effects of these disturbances in the Caribbean are alarming [10, 17, 30, 31], and a local assessment is urgently needed to determine the impact on the coral assemblage and their distribution along the depth gradient, as it will shape not only the physical structure of the reef but also that of the whole community.

2 Materials and methods

2.1 Study area

Chinchorro Bank Biosphere Reserve is located within 18°48′44.24″ N, 87°28′28.27″ W; 18°48′46.03″ N, 87°12′01.85″ W; 18°21′39.10″ N, 87°11′59.95″ W; 18°21′37.36″ N, 87°28′23.77″ W (Fig. 1a) and is the largest atoll reef in the Caribbean with a total area of more than 700 km^2 [32]. The depth range and the coral coverage decrease from south to north [32, 33]; in the southern area, numerous reef patches and coral ridges are observed, while in the northern area, there are no ridges, and coral patches are concentrated mainly in the center of the lagoon [18, 32, 33]. The area is influenced by the oceanic and coastal currents of the Caribbean and by the meteorological phenomena of the region and the Atlantic [34]. The substrate in this area consists of sedimentary limestone, which is highly susceptible to water erosion [35]. The average

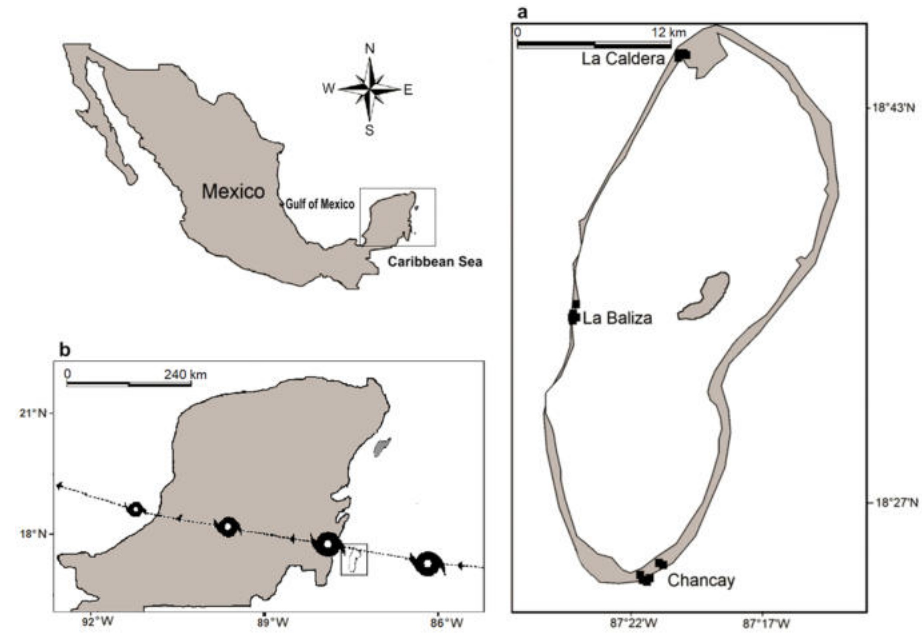


Fig. 1 Study area, Chinchorro Bank Biosphere Reserve. **a** The monitoring sites (La Caldera, La Baliza, and Chancay) and the sampling locations in each site are marked; **b** The Trajectory of Hurricane Dean, represented with a dotted black

annual precipitation exceeds 1450 mm [18]. In addition, this reef is exposed to atmospheric meteors such as tropical storms and hurricanes between June and November [36].

Three monitoring sites were selected, each with different depths, reef development, and levels of anthropogenic pressure derived from regulated fishing and ecotourism activities: (1) La Caldera, a shallow site (3–12 m) with coral patches dominated by submassive coral species of the genus *Orbicella,* and with fishing pressure; (2) La Baliza, located in the central-western region, is characterized by both shallow and deep reefs (3–21 m) and degree of human disturbance as the NPA zonification allows regulated fishing and tourist activities (e.g., snorkeling and diving) and, (3) In the extreme south, Chancay has coral ridges of *Agaricia tenuifolia*, numerous coral patches, and shallow and deep reefs (7–25 m), with no evidence of alteration by anthropogenic activities (Fig. 1a) [18, 33].

2.2 Data collection and analyses

The sampling design was hierarchical and balanced. Four monitoring periods (April 2007 (before the hurricane), October 2007(immediately after the hurricane), April 2009 (after the hurricane), and December 2009 (after the hurricane) and two spatial scales were considered: three sites (La Caldera, La Baliza, and Chancay), and six sampling locations (six per site). A total of 360 video transects parallel to the coast (50 x ~ 0.6 m) were recorded at 0.4 m from the bottom [37]. Each video frame covered an area of ~ 0.6 × 0.4 m. Transects were deployed along the depth gradient at each site. The sampling effort consisted of five video transects per location, with six sampling locations per site, repeating in each of the four sampling periods (n = 5 transects/locations/sites/period × 6 locations × 3 sites × 4 periods). Depth was recorded with a dive computer, and the topographic complexity of each transect was assessed using a 10-m chain [38]. Depth ranges were classified as shallow (< 12 m) and deep (> 12 m), based on local bathymetry and site conditions. La Caldera, a shallow area (3–12 m), was used as a reference site to characterize the shallow zone (< 12 m), while La Baliza and Chancay included both shallow (≈ 3 m) and deeper areas, reaching depths of up to 25 m.

Each video transect was analyzed on a high-resolution monitor using systematic random sampling, in which 40 video frames and 50 points per frame (2000 points per video transect) were examined. This analysis allowed us to record the richness and coverage of hermatypic corals, as well as the benthic components classified as follows: macroalgae, sponges, hydrocorals, octocorals, turf, articulated calcareous algae, crustose coralline algae, seagrass, sand, rocks, rubble, and calcareous pavement [39]. The classification of the morpho-functional groups of corals (semispherical, submassive, encrusting, branching, brain, etc.) was carried out following the criteria established by Arias-González et al. [37].

The sampling effort was assessed using sample-based rarefactions and the ICE, Chao 2, Jackknife 1, and Jackknife 2 estimators. Curves were generated with 10,000 random combinations using the EstimateS V.9 program [40]. Richness (S) and Shannon diversity (H′, in nats) were used to assess the structure of the hermatypic coral assemblage at both the species and morpho-functional group levels. Statistical comparison of these attributes and total live coral coverage was performed with permutational analyses of variance (ANOVA), based on Euclidean distance matrices [41], using two experimental designs. The first is a three-way design with crossed and nested factors. The factors considered were: (i) Sampling time (Ti) with four levels (April 2007, October 2007, April 2009, and December 2009) and fixed effect; (ii) Sites (Si) with three levels (La Caldera, La Baliza, and Chancay) and fixed effect; (iii) Locations (Lo) with 18 levels (six locations per site) and random effect. The second is a three-way design with crossed factors and fixed effects. The factors considered were: (i) Sampling time (Ti) with four levels (April 2007, October 2007, April 2009, and December 2009); (ii) Sites (Si) with two levels (La Baliza and Chancay); (iii) Zones (Zo) with two levels [shallow (≤ 12 m) and deep (> 12 m)].

The models were:

$$Y = \mu + Ti_i + Si_j + Lo_k\left(Si_j\right) + Ti_i x\, Si_j + Ti_i x\, Lo_k\left(Si_j\right) + \varepsilon_{ijk} \tag{1}$$

$$Y = \mu + Ti_i + Si_j + Zo_k + Ti_i x\, Si_j + Ti_i x\, Zo_k + Si_j x\, Zo_k + Ti_i x\, Si_j x\, Zo_k + \varepsilon_{ijk} \tag{2}$$

where Y is the predictor variable, μ is the mean, and $\mathcal{E}_{ijk}$ is the cumulative error.

The change in composition and cover of coral species and morpho-functional groups across sites, years, and zones was compared with permutation-based multidimensional analysis of variance (PERMANOVA). Therefore, data were previously transformed with a fourth root to construct Bray–Curtis similarity matrices, following the designs mentioned in the previous paragraphs. The statistical significance of all permutational ANOVAs and PERMANOVAs was tested with 10,000 permutations under a reduced model, using type III (partial) sum of squares (SS) [41].

The contribution of coral species and morpho-functional groups was estimated with similarity percentage analysis (SIMPER), considering a cutoff point of 65%. To graphically show the changes in the composition and coverage of coral species and morpho-functional groups between sampling locations, zones, and sites in the analyzed periods, ordinations were made with principal coordinate analysis (PCO). The same pretreatment and resemblance coefficient of PERMANOVA was carried out for SIMPER and PCO. All permutational ANOVAs, PERMANOVA, SIMPER, and PCO were performed with PRIMER V6.1 + PERMANOVA 1.11 software [41, 42].

The relationship between the composition and coverage of coral species and morpho-functional groups with benthic structure variables was analyzed based on canonical redundancy analysis (RDA), assuming a short environmental gradient and a linear relationship. Biological variables were transformed to the fourth root, and environmental variables were normalized to Z values. For selecting environmental variables, those with a correlation less than 0.75 and a VIF < 10 were considered to reduce multicollinearity, following the criteria of Legendre and Legendre [43]. Statistical significance was tested based on 10,000 permutations under a reduced model in CANOCO v. 4.5 [44].

3 Results

The four monitoring campaigns recorded 32 hermatypic coral species belonging to 10 families and 11 morpho-functional groups (Supplementary Material, Table A1). Sample-based rarefactions evidenced a sampling effort with a representativeness of 94 to 100% (Supplementary Material, Fig. A1).

3.1 Coral cover

Total live coral cover (LCC) showed a significant spatio-temporal variation, mainly at the level of locations nested by sites (Table 1, Model 1). La Caldera harboured the highest coverage throughout the period analyzed, with an average of 11.36%. In contrast, La Baliza site presented the lowest values with an average value of 3.8% (Fig. 2e). At the temporal level, a decrease in LCC was recorded in October 2007 after Hurricane Dean's passage (La Caldera = 23.7%, La Baliza = 43.3%), which was accentuated in 2009, especially in La Baliza (55%) locations (Fig. 2a).

Furthermore, when shallow and deep zones were incorporated into the analysis using Model 2, significant differences were detected only at Chancay, where live coral cover was higher in shallow zones (9.5% LCC) compared to deeper zones (5.1% LCC; Fig. 2b). In the temporal analysis, significant losses of live coral cover were recorded in shallow zones across Banco Chinchorro, with an initial reduction of 25.6% after the hurricane and a 40.2% decline by December 2009; while deeper zones did not show significant changes (Fig. 2c).

3.2 Diversity

In Model 1, the average richness and Shannon diversity at the level of coral species and morpho-functional groups showed significant spatio-temporal variation at the Locations (Sites) and Time x Sites level, where the factors related to spatial variation had higher values of the components of variation, followed by the Time factor (Table 1). The average richness of coral species and morpho-functional groups (MFG) in Chinchorro Bank presented limited spatial variation among locations (Figs. 3a and 4a). However, locations in La Caldera showed higher average values of species richness ($\overline{S} = 8.4$) (Fig. 3a) and morpho-functional groups ($\overline{S} = 5$) (Fig. 4a). Regarding Shannon diversity, high variation was observed between locations, with no evident spatial pattern between sites (Table 1; Figs. 3c, 4c).

After Hurricane Dean, a significant change was detected in La Caldera and La Baliza, with a decrease in richness (Fig. 3b [at the specie level: La Caldera = 21.9%, La Baliza = 42.6%], Fig. 4b [at the MFG level: La Caldera = 20.7%, La Baliza = 35.4%]) and Shannon diversity (Fig. 3d [at the specie level: La Caldera = 15.3%, La Baliza = 37.5%], Fig. 4d [at the MFG level: La Caldera = 18.6, La Baliza = 38.3%]), particularly La Baliza was the most affected. It is noteworthy that, although La Caldera had an initial reduction in richness and Shannon diversity of species, it showed a remarkable recovery in 2009, reaching values similar to those recorded before the event ($\overline{S} = 9.1$, H′ = 1.3; Fig. 3b, 3d). In contrast, Chancay did not show significant differences in diversity in any of the periods sampled, neither at the level of species nor morpho-functional groups (Fig. 4d).

Model 2, which included depth as a variable, the richness of species, and morpho-functional groups, showed significant differences between shallow and deep zones in Chancay. Specifically, the richness of species was higher in deeper zones ($\overline{S}$= 6.8), while that of morpho-functional groups was higher in the shallow zones ($\overline{S}$= 4.9) (Fig. 5a, c). In addition, morpho-functional groups' richness decreased significantly after Hurricane Dean (≥ 25%) without evidence that indicates a recovery to pre-event conditions ($\overline{S}$= 3.9; Fig. 5d). Additionally, Shannon diversity for species showed significant temporal variation only in La Baliza, where shallow and deep zones markedly decreased in the post-hurricane period [shallow (52.2%) vs. deep (29.4%)] (Fig. 5b). Also, the diversity of morpho-functional groups decreased in both shallow and deep zones after the event [shallow (36.3%) vs. deep (18.1%)], although the shallow zone was the only with evidence of recovery reachingvalues similar to the hurricane (MFG, H′ = 1; Fig. 5e).

3.3 Community structure

The composition and coverage of coral species and morpho-functional groups varied significantly in all factors considered in the experimental design. The major explanation of variance in the model corresponded to the spatial factors of Locations and Sites, followed by Time (Table 1). The PCO ordination analyses at the sites scale revealed an evident dissimilarity between sites, especially at the species level, with Chancay standing out as the most differentiated (Fig. 6a). However, the PCO based on morpho-functional groups showed an overlap between the Chancay locations and those of the other sites (Fig. 6b). SIMPER analysis indicated that the main species that explained the dissimilarity between locations in each site were *Orbicella faveolata*, *Pseudodiploria strigosa*, *Montastraea cavernosa*, *Siderastrea* spp., *Orbicella annularis*, *Porites astreoides* and *P. furcata*, which include brain, semispherical, submassive and digitiform corals (Supplementary Material, Tables A5 and A6). Specifically, *P. strigosa* and *O. faveolata* contributed to the differences between locations at La Caldera; *O. faveolata and O. annularis* at La Baliza; and *A. tenuifolia* at Chancay (Supplementary Material, Table A5).

The PERMANOVA and PCO outputs of the Time × Sites interaction showed the impact of Hurricane Dean on coral composition and coverage at Chinchorro Bank. At La Caldera, the major change was recorded in October 2007, with significant differences concerning the other periods sampled (Fig. 6c, d; Supplementary Material, Table A2). This change was associated with a decrease in the coverage of foliose (93.1%) and digitiform corals (68%), particularly *Agaricia tenuifolia* (93.1%) and *Porites furcata* (85%) (Supplementary Material, Tables A7 and A8). La Baliza was the most affected

Table 1 Permutational ANOVAs and PERMANOVA outputs of the variation of the assemblage structure of coral species and morpho-functional groups (MFG) in Chinchorro Bank, Mexico

Anova																Permanova					
	S (species)			H' (species)			LCC			S (MFG)			H' (MFG)			CC (species)			CC (MFG)		
F	PF	P	CV	PF	P	CV	PF	P	CV	PF	P	CV	PF	P	CV	PF	P	CV	PF	P	CV
Model 1																					
Ti	19.17	**0.0001**	16.2	9.15	**0.0001**	14.8	7.38	**0.0002**	9.7	20.90	**0.0001**	16.9	7.61	**0.0003**	12.5	4.15	**0.0001**	7.2	4.84	**0.0001**	7.9
Si	13.61	**0.001**	21.9	0.17	0.8432	0.0	12.88	**0.0017**	30.3	8.10	**0.0057**	19.3	4.15	**0.0401**	11.3	9.61	**0.0001**	23.6	5.73	**0.0005**	19.2
Lo(Si)	3.65	**0.0001**	12.8	4.67	**0.0001**	18.2	11.62	**0.0001**	20.6	4.29	**0.0001**	15.5	3.06	**0.0002**	12.8	6.44	**0.0001**	18.1	8.02	**0.0001**	20.2
TixSi	3.63	**0.0043**	10.7	3.20	**0.0104**	13.3	1.03	0.4143	1.1	3.36	**0.007**	10.1	3.33	**0.0075**	12.8	2.55	**0.0001**	8.8	3.28	**0.0001**	10.6
TixLo(Si)	1.04	0.4161	35.3	1.35	0.078	11.2	1.65	**0.0084**	10.2	0.88	0.6861	0.0	1.34	0.0826	10.4	1.24	**0.0099**	7.6	1.27	**0.0277**	7.9
Residual			3.2			42.5			28.1			38.3			40.3			34.7			34.1
Model 2																					
Ti	8.29	**0.0001**	15.2	7.20	**0.0003**	10.2	6.05	**0.001**	8.4	9.53	**0.0001**	15.7	7.79	**0.0001**	13.4	2.77	**0.0002**	5.8	3.60	**0.0003**	6.8
Si	0.07	0.7901	0.0	0.11	0.7449	0.0	62.21	**0.0001**	21.2	11.32	**0.0003**	12.5	2.47	0.1205	4.5	46.75	**0.0001**	21.4	21.05	**0.0001**	13.7
Zo	2.59	0.1128	5.1	14.52	**0.0002**	10.9	31.73	**0.0001**	15.0	6.61	**0.0109**	9.2	2.41	0.1269	4.4	20.18	**0.0001**	13.9	21.72	**0.0001**	13.9
TixSi	3.27	**0.0234**	12.0	7.14	**0.0007**	14.3	0.98	0.4055	0.0	1.52	0.2102	5.5	5.43	**0.0016**	15.3	1.74	**0.0262**	5.3	2.74	**0.0013**	7.9
TixZo	1.88	0.1333	7.4	5.23	**0.0011**	11.9	4.10	**0.0085**	9.3	1.54	0.2014	5.6	3.41	**0.0176**	11.3	1.88	**0.0113**	5.8	1.59	0.1104	4.6
SixZo	5.50	**0.0196**	12.2	9.26	**0.0029**	12.0	13.63	**0.0006**	13.6	7.75	**0.0055**	14.3	1.43	0.2341	3.5	16.11	**0.0001**	17.4	20.11	**0.0001**	18.9
TixSixZo	1.57	0.1874	8.5	3.12	**0.0238**	11.9	1.74	0.1587	6.4	0.93	0.4266	0.0	2.29	0.0761	11.7	0.90	0.5915	0.0	1.38	0.1923	5.2
Residual			39.6			28.7			26.1			37.2			35.8			30.4			29.2

S = richness, H′ = Shannon diversity, LCC = total live coral cover, CC = composition and cover, F = factor, PF = pseudo-F, P = P-value, CV = variation component (%), Ti = time, Si = sites, Lo(Si) = locations nested in sites, and Zo = zones

P-values in bold correspond to significant differences (P ≤ 0.05)

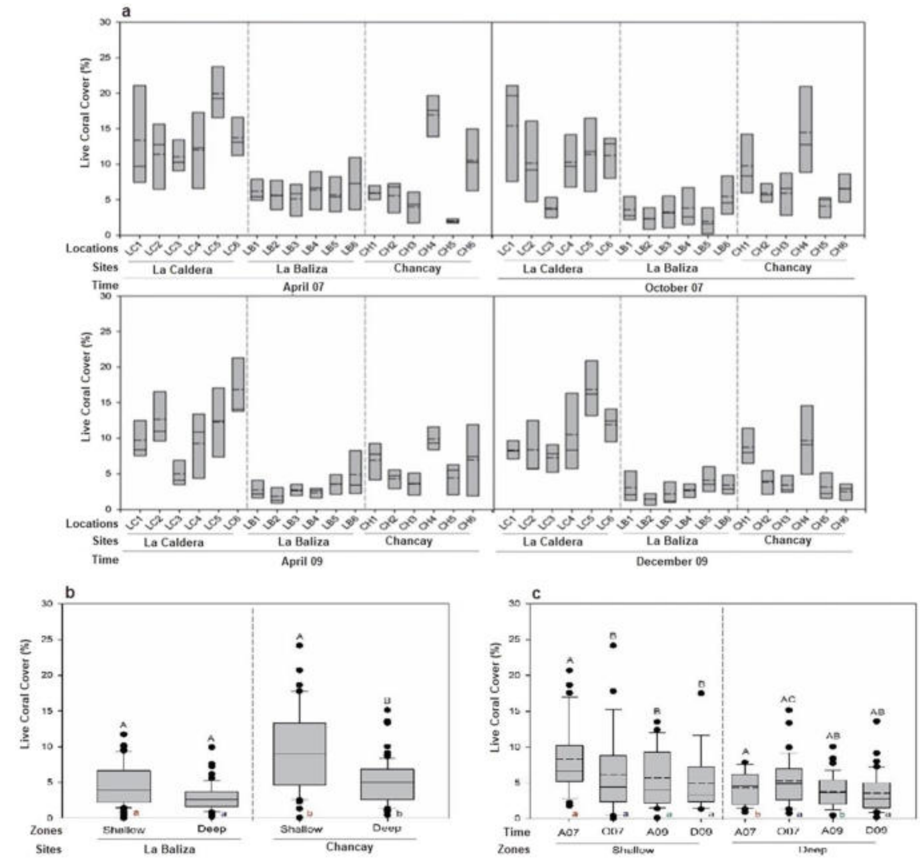


Fig. 2 Spatio-temporal variation: **a** Live coral coverage at the level of time and nested locations in sites; **b** Live coral coverage at the level of sites x zones; **c** Live coral coverage at the level of zones x time. Inside each box, the solid line represents the median, and the dotted line corresponds to the mean. Codes: LC = La Caldera, LB = La Baliza, CH = Chancay, A07 = April 2007, O07 = October 2007, A09 = April 2009, D09 = December 2009. The black capital letters represent the sites x zones, through zones (**b**), zones x time, through time (**c**). The lowercase letters represent the sites x zones through the sites (**b**), zones x time through zones (**c**)

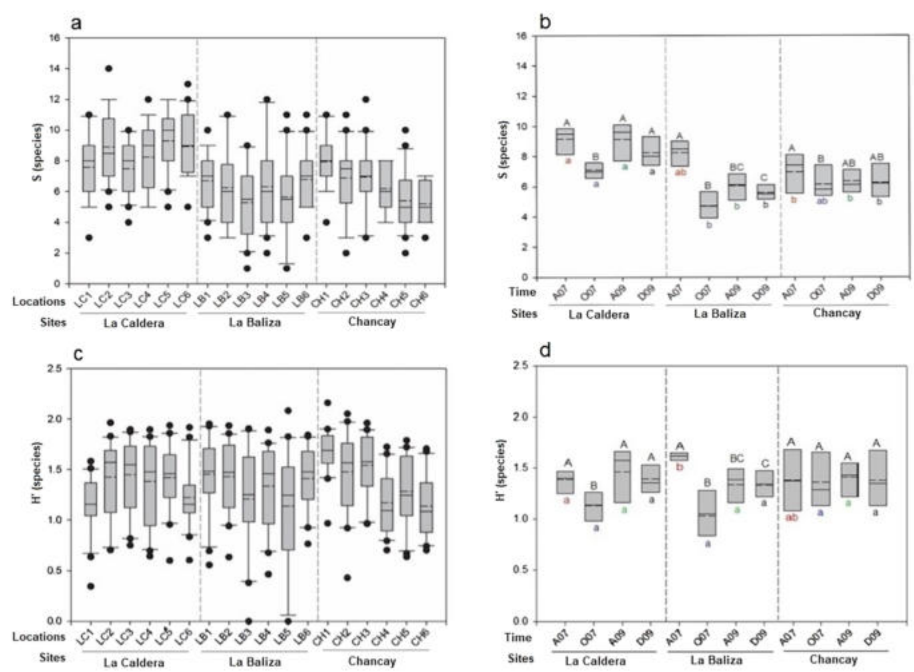


Fig. 3 Spatio-temporal variation: **a** coral species richness at the level of nested locations in sites and **b** at the level of sites x time; **c** Shannon diversity of coral species at the level of nested locations in sites and **d** at the level of sites x time. Inside each box, the solid line represents the median, and the dotted line corresponds to the mean. Codes: LC = La Caldera, LB = La Baliza, CH = Chancay, A07 = April 2007, O07 = October 2007, A09 = April 2009, D09 = December 2009. The capital letters represent differences based on time x sites over time, and the lowercase letters represent differences based on time x sites across sites

site, as a result of the decrease in the cover of *Pseudodiploria strigosa* (69.5%), *Colpophyllia natans* (46.1%), and *Diploria labyrinthiformis* (41.6%) immediately after the hurricane (October 2007); and a loss of 84%, 100% and 83.3% respectively, at the end of the study (December 2009) (Fig. 6c, d; Supplementary Material, Tables A2, A7, A8). In contrast, Chancay

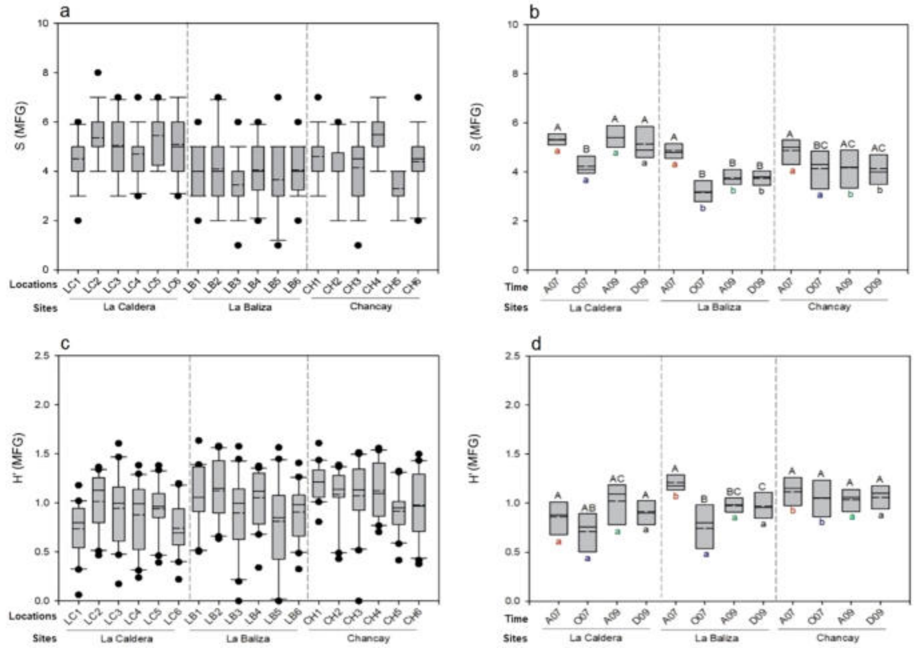


Fig. 4 Spatio-temporal variation: **a** richness of coral morpho-functional groups at the level of nested locations in sites and **b** at the level of sites x time; **c** Shannon diversity of coral morpho-functional groups at the level of nested locations in sites and **d** at the level of sites x time. Inside each box, the solid line represents the median, and the dotted line corresponds to the mean. The capital letters represent differences based on sites x time across time, and the lowercase letters represent differences based on sites x time across the sites

did not show significant temporal changes in the structure of the coral assemblage after the hurricane (Fig. 6c, d; Supplementary Material, Table A2).

The RDA ordination showed a higher coverage of submassive (8.1%) and brain corals(0.8%), especially *O. annularis* (6.3%), *D. labyrinthiformis* (0.2%), and *P. strigosa* (0.5%) in La Caldera. At Chancay, there was relatively higher coverage of crustose coralline algae (2.1%), articulated calcareous algae (2.2%), and sponges (5.6%), along with a greater presence of foliose (4.8%), digitiform (1%), and branching corals (0.2%) compared to the other sites. Notable species at Chancay included *Agaricia tenuifolia* (1.6%), *P. furcata* (0.35%), and *Acropora palmata* (0.09%). In contrast, the La Baliza locations were more strongly associated with higher proportions of coral rubble (2%), sand (27.8%), and turf (35%), and showed relatively higher coral coverage of *Agaricia agaricites* (0.62%) than the other sites (Fig. 7a, b).

The composition and coverage of species and morpho-functional groups differed between shallow and deep zones in Chancay, while in La Baliza, differences were observed only at the species level (Table A3). SIMPER routine showed that *P. astreoides*, *O. faveolata,* and *M. cavernosa* mainly explained the differences between shallow and deep zones (Supplementary Material, Tables A9 and A10). In the shallow zone, the coral assemblage changed significantly after the hurricane, with subsequent samplings (October 2007 to December 2009) different from those in April 2007. Although no immediate change was detected in the deep zone, differences were observed between October 2007 and the last two samplings (April 2009 and December 2009; Fig. 6e; Supplementary Material, Table A4). In the shallow zones, *A. tenuifolia, O. faveolata,* and *O. annularis* contributed to the dissimilarities with decreased coverage after the tropical cyclone (October 2007 to December 2009). In the deep zone, *O. faveolata, P. astreoides,* and *M. cavernosa* were key species in explaining the differences between periods, with a higher cover of *O. faveolata* (1.3%) in October 2007 and an increase of 7.6% in *M. cavernosa* towards the end of the study (December 2009) (Supplementary Material, Table A11).

Species-level RDA ordination showed that live coral coverage was highest in shallow zones (6.5%), particularly in April 2007 (8.2%), associated with *Acropora cervicornis* (0.06%), *D. labyrinthiformis* (0.09%), and *O. annularis* (0.8%). After Hurricane Dean, the cover of coralline crustose algae and *P. astreoides* increased 111% and 96% respectively in the shallow zone. Other representative species in the shallow zone were *A. palmata* (0.1%), *A. tenuifolia* (1.9%), and *P. furcata* (0.4%). In contrast, the deep zones showed less early variability in the structure of the coral assemblage and did not show a clear effect of the hurricane. These zones were characterized by a higher coverage of macroalgae (26.3%), sponges (4.8%), and higher topographic complexity ($C=0.27$), as well as by the presence of *M. cavernosa* (0.5%), *M. meandrites* (0.1%), *Siderastrea* spp. (0.8%), *P. divaricata* (0.03%), *A. agaricites* (0.76%), *C. natans* (0.05%), and *O. faveolata* (0.7%) (Fig. 7c).

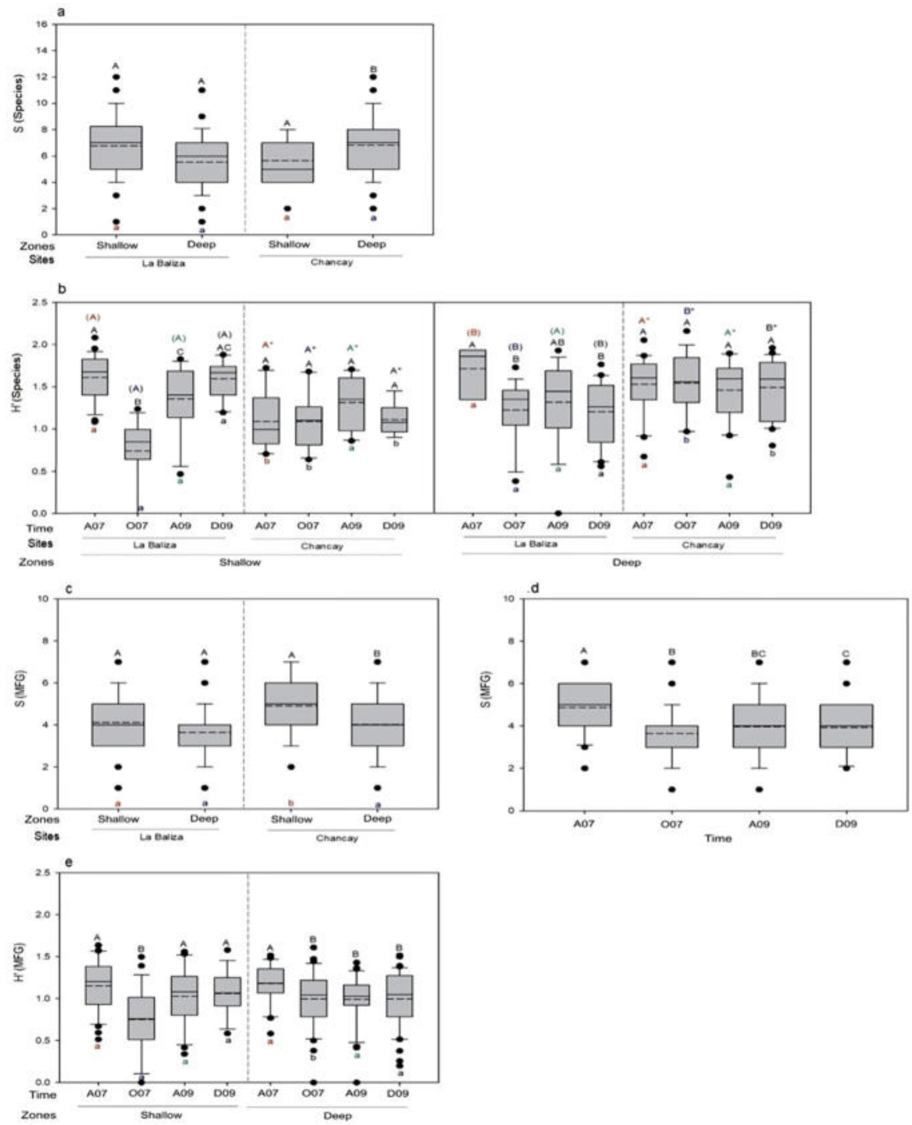


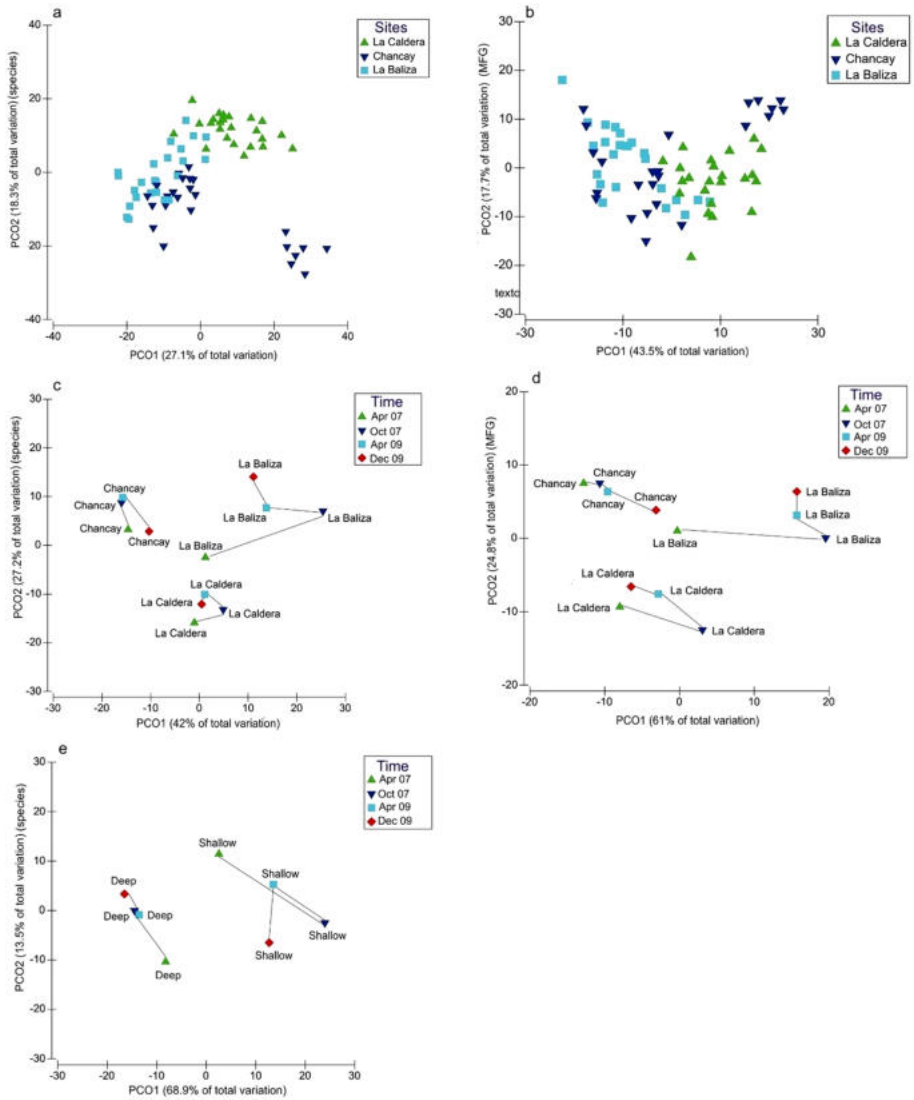
Fig. 5 Spatio-temporal variation: **a** coral species richness at the level of sites x zones; **b** Shannon's diversity of coral species at the level of zones x sites x time; **c** Richness of coral morpho-functional groups at the level of sites x zones; **d** richness of coral morpho-functional groups at the level of time; e Shannon diversity of coral morpho-functional groups at the level of zones x time. The solid line represents the median, and the dotted line corresponds to the mean. The black capital letters represent the sites x zones, through zones (**a**, **c**), zones x time, through time (**e**), and depth x sites x time, through time (**b**). The lowercase letters represent the sites x zones through the sites (**a**, **c**), zones x time through zones (**e**), and zones x sites x time through the sites (**b**). In **b**, the colored capital letters with parentheses indicate zones x sites x time, through zones for La Baliza; the colored capital letters with asterisks represent the same test for Chancay

4 Discussion

Meteorological events such as storms and hurricanes affect the coral reefs with differences in regional and local scales, depending on the trajectory, and potential changes in their intensity [45]. These seasonal phenomena are essential to the dynamics of the coral areas as they contribute to vertical mixing and circulation within the water column, which prevents the accumulation of sediments, reduces excessive concentrations of inorganic nutrients, and can mitigate elevated temperatures during thermal stress events [46]. However, as their intensity increases with the current climate change scenario, they are now considered destructive stressors that, besides causing major habitat fragmentation, can also spread diseases [16, 47]. This was demonstrated as Hurricane Dean impacted and modified the structure of the coral assemblage at the level of species and morpho-functional groups in Chinchorro Bank reef, showing significant spatial variation at the sites and locations level and through depth change; therefore, the same stressor had a different impact at the micro-scale level.

Despite the impact of Hurricane Dean, the La Caldera site presented the highest average values of species richness and live coral coverage in Chinchorro Bank. This pattern is characteristic of coral reefs, where sites with higher species richness also tend to show higher coral coverage [48, 49], evidencing a significant relationship between these community attributes. In addition, it was characterized by the highest cover of submassive and brain corals, which, due to their morphology and size, are major contributors to the coral coverage [1, 50]. The structural conformation of the site shows

Fig.6 PCO ordinations showing **a** spatio-temporal variation of coral composition and cover based on nested locations in the sites at the level of specie and **b** morpho-functional groups, **c** PCO based on sites x time at the level of specie, and **d** EMF and **e** PCO based on zones x time at the level of specie



the higher average richness of morpho-functional groups, which was positively correlated with the average richness of coral species, contributing to the diversity of ecological traits and functions within the ecosystem [51].

The second site with the highest coral coverage was Chancay; however, it also recorded a high cover of coralline crustose algae. The CCA is a benthic element that may favor both coral development and reef cementation due to their calcium carbonate production [52], and it may promote the settlement of coral planula larvae by emitting specific chemical signals [53]. Particularly in the shallow zone of Chancay, spurs and grooves structures are mainly composed of foliose and branching corals, resulting in an increase in coral coverage and an enhancement of the structural heterogeneity of the reef habitat. In contrast, La Baliza showed a higher coverage of sandy substrate, characterized as a soft and unstable bottom that hinders the settlement and development of corals [1]; therefore, this site not only registered the lowest live coral coverage, but the presence of species that develop small colonies, such as *Agaricia agaricites*.

La Baliza and Chancay were the only sites with a depth range and shallow and deep reef development. Still, only Chancay showed significant differences between both zones regarding species richness, diversity of morpho-functional groups, and live coral cover. The deeper zone presented higher species richness as deep reefs are less exposed to disturbances such as storms, hurricanes, and thermal stress [54, 55]. The contrary effect was recorded in the shallow zones; however, rather than only the effect of any tropical cyclone, the lower species richness observed was due to the dominance of *Agaricia tenuifolia* and *Porites furcata*, which are fast-growing species with high tolerance to environmental stress and morphologies that can resist high hydrodynamic conditions [54, 56, 57]. In addition, the growth strategy of

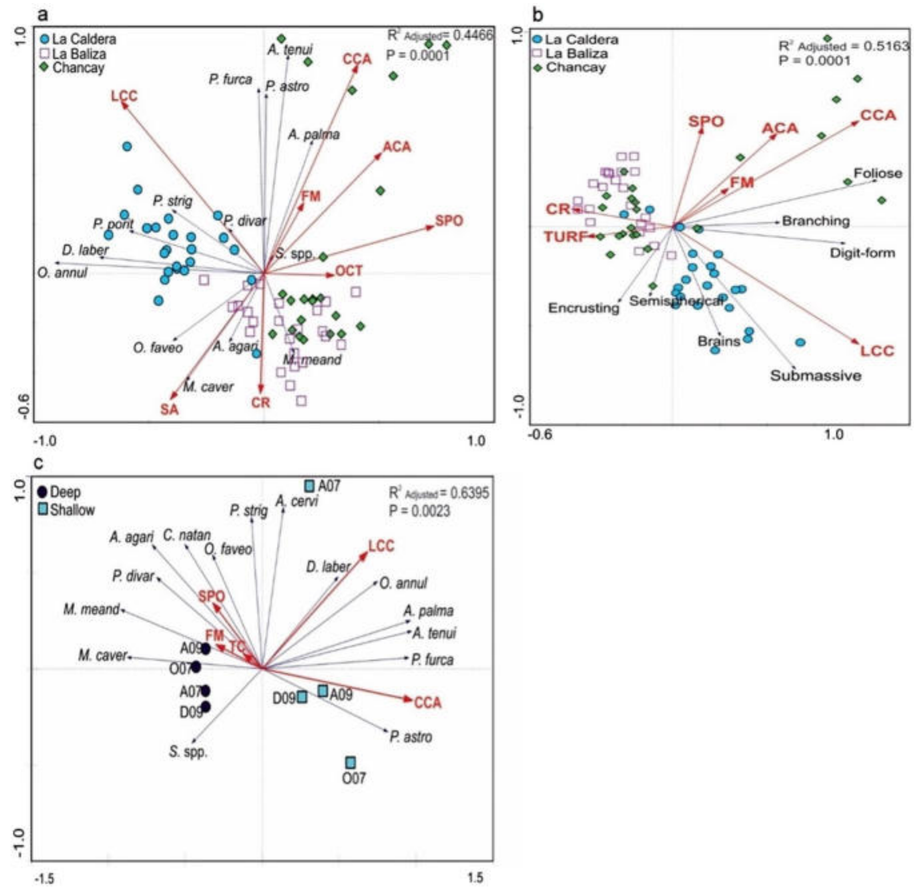


Fig. 7 RDA triplot of the relationship between the composition and cover of coral species *vs*. the elements of the benthic habitat. Analysis of nested locations in sites x time (**a**); Zones x time (**c**), RDA ordination of the relationship between the composition and coverage of coral morpho-functional groups *vs*. the elements of the benthic habitat of the nested locations in sites x time (**b**). Codes: CCA = crustose calcareous algae, ACA = articulated calcareous algae, FM = fleshy macroalgae, CR = Coral rubble, SA = sandy substrate, TC = topographic complexity, LCC = live hermatypic coral, OCT = octocorals, SPO = sponges. Coral species are denoted as the genus's initial and the species' first five letters

both species may limit the recruitment and development of less competitive coral species [58], resulting in a high coral coverage but a monospecific reef.

Another characteristic of Chinchorro Bank's benthic assemblage is the higher cover of sponges and macroalgae at deeper zones, coinciding with a low abundance of omnivorous and herbivorous fish [59, 60]. These conditions favor the development of such organisms due to the available space and reduced grazing pressure [54, 61], which decreases the competition and promotes their proliferation and a high architectural complexity, usually associated with shallow reefs where the abundance of submassive and branching usually increases the structural heterogeneity [11, 64]. In addition, sponges, in particular, tend to thrive in deep zones, where there is a higher availability of dissolved nutrients in the water column, which are indispensable for their feeding and growth [62, 63]. While this may appear to represent a contradictory pattern, the benthic irregular geological structures, consolidated coral matrix, as well as the abundance of sponges, soft corals, and other structuring organisms, had a higher contribution to the topographic complexity than only a high coverage of reef-building corals [65, 66].

However, a different scenario between shallow and deep reefs is evident in Chinchorro Bank after the effect of Hurricane Dean. Tropical cyclones have historically played a crucial role in shaping reef ecosystems by modifying their structure and functioning [8, 31]. Shallow reef zones throughout Chinchorro Bank, showed a considerable loss of live coral coverage (25.6%), with no apparent signs of recovery in subsequent years, evidencing that shallower reefs are more vulnerable to hurricane-induced wave force and sediment resuspension, causing injuries and abrasion to the coral tissue, which may decrease their resistance and promote a high mortality [10, 55, 67]. Furthermore, this effect is observed in particular species, with a decrease in the abundance of *Agaricia tenuifolia*, *O. annularis,* and *O. faveolata*, followed by a significant increase in *Porites astreoides*. Species of the genus *Orbicella* have been documented to have low tolerance to high suspended sediment levels [68] and limited ability to recolonize due to their low growth rates and sexual recruitment [8, 69, 70]. In addition, *Agaricia* and *Orbicella* polyps possess thin tissues, increasing their susceptibility to physical damage, particularly in the case of foliose morphology, to fragmentation [71–74]. Therefore, opportunistic species such as *P. astreoides* will thrive in disturbed environments [75] as this hermaphroditic species is capable of self-fertilization, being able to thrive even in conditions of low colony density [76], and its seedlings present a high dispersal capacity both horizontally and vertically [77].

Furthermore, the site's local characteristics should be considered, as they may drive differential responses to the same stressor. La Baliza was the most affected site, presenting the highest loss of live coral cover, richness, and diversity, particularly of the species *O. annularis*, *O. faveolata, Pseudodiploria strigosa, Colpophyllia natans,* and *Diploria labyrinthiformis*, with no evidence of significant recovery. In La Caldera, the coverage of *M. cavernosa, A. tenuifolia,* and species of the genus *Siderastrea* decreased significantly; however, two years later (by December 2009), recovery in species richness was recorded. Chancay, in particular, stood out as the most resistant site since its coral composition and coverage, both in taxonomic and morpho-functional terms, remained stable after the event. The variability in sites response appears to be influenced by a combination of factors, including reef health, depth, and the trajectory of Hurricane Dean, which passed directly over the northern sector of Chinchorro Bank (Fig. 1b); consequently, northern and central sites such as La Caldera and La Baliza experienced the direct and strongest impacts, while the southern site, Chancay, was relatively less affected not only due the trajectory of the huricane but also, are inherently sheltered as the coral distribution is in deeper areas. Moreover, it has been suggested that degraded reefs or reefs with low coral coverage exhibit lower resilience and higher vulnerability to disturbance [78], coinciding with the pattern recorded at La Baliza. In addition to these key factors, other elements can also influence the reef resistance and more important their ability to recover or resilience, such as: (i) the availability of suitable substrate for the settlement of new corals [71, 79]; (ii) the vulnerability of the dominant species [80]; and (iii) the reproductive strategies of the species present, along with their growth and recruitment rates, which determine their ability to recolonize and maintain reef structure following disturbance [8, 69, 70].

The impact of Hurricane Dean along the Atoll could also be related to the changes in the morpho-functional diversity of the hermatypic corals. At La Caldera, the abundance of foliose and digitiform corals decreased, while branching corals increased. At La Baliza, the coverage of brain and submassive corals decreased, with a parallel increase in semispherical corals. This morpho-functional change observed at Chinchorro Bank is consistent with recent trends documented in the Caribbean, with a constant decline of brain and submassive, which are progressively being replaced by semispherical forms that contribute less to the cover and structural complexity of the reef [65, 75, 81]. Additionally, branching corals are particularly susceptible to the physical impact of waves, resulting in two possible outcomes: mortality of fragments or the generation of new colonies through asexual reproduction, provided that the substrate and conditions allow it [71, 72, 82].

At Chinchorro Bank, a decrease in coral richness, morpho-functional groups, and live coral coverage was observed, consistent with that reported in other Caribbean regions impacted by hurricanes. However, the magnitude of the impact varied by sites and zones. Differences between sites are attributed to variability in coral structure, composition, and coverage, while differences between zones are related to the degree of exposure to tropical cyclones. In this context, the lower impact recorded in deeper areas highlights the role of depth in modulating disturbance impacts and supporting reef recovery. Although this study reflects conditions from 18 years ago, over the past decade, eight category 5 hurricanes have affected the Caribbean region, recording at least two of these events in the last three years and is forecasted to even increase under climate change scenarios [83]. Therefore, it is important to consider the timelines of the effects that these tropical cyclones will have not only in Chinchorro Bank, but as a broader approach to understand in a global context, the reef resilience and recovery dynamics.

Despite its geographic vulnerability due to its constant exposure to storms and hurricanes, Chinchorro Bank, with its combination of shallow and deep reefs, could show a certain degree of resilience, provided that the influence of direct human pressures, such as urban development, overfishing, or coastal pollution, is limited. However, in recent years, the incidence of coral diseases has been reported, a phenomenon that the passage of hurricanes may aggravate. This puts even natural refuges at risk and raises questions about the fate of these ecosystems, whose persistence will depend on the balance between their resilience and the intensity of the stressors they face in the coming decades.

5 Author contributions.

Conceptualization, CdAG, FARZ, APRT; methodology, CdAG, FARZ, APRT; validation, CdAG, FARZ, APRT; formal analysis, CdAG, FARZ, APRT; investigation, CdAG, FARZ, APRT; resources, FRRZ, MCGR; writing—original draft preparation, CdAG, FARZ, APRT; writing—review and editing, CdAG, FARZ, APRT; visualization, CdAG, FARZ, APRT; funding acquisition, FARZ, MCGR. All authors have read and agreed to the published version of the manuscript.

Acknowledgements The authors thank the Comisión Nacional de Áreas Naturales Protegidas (CONANP) authorities for their support and assistance during fieldwork.

Author contributions Conceptualization, CdAG, FARZ, APRT; methodology, CdAG, FARZ, APRT; validation, CdAG, FARZ, APRT; formal analysis, CdAG, FARZ, APRT; investigation, CdAG, FARZ, APRT; resources, FRRZ, MCGR; writing—original draft preparation, CdAG, FARZ, APRT; writing—review and editing, CdAG, FARZ, APRT; visualization, CdAG, FARZ, APRT; funding acquisition, FARZ, MCGR. All authors have read and agreed to the published version of the manuscript.

Funding CAG received a scholarship (I.D. 484750) from Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI) while conducting the study and writing the manuscript. The present research was funded by the World Wildlife Fund (WWF)-Mexico, the Comisión Nacional de Áreas Naturales Protegidas (CONANP), and Universidad de Guadalajara.

Data availability The raw data used in this study are available to the corresponding author upon request. It is important to point out that all the synthesized results necessary to interpret the findings are included within the manuscript and supplementary materials.

Declarations

Ethical approval consent to participate The present study does not involve manipulating or sampling any organism; no ethical approval is required. Not applicable.

Consent for publication The authors consent to the publication of the present manuscript.

Competing interest The authors declare no competing interests.

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