Geomorphically controlled coral distribution in degraded shallow reefs of the Western Caribbean

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ABSTRACT

The development of coral reefs results from an interaction between ecological and geological processes in space and time. Their difference in scale, however, makes it difficult to detect the impact of ecological changes on geological reef development. The decline of coral cover over the last 50 years, for example, has dramatically impaired the function of ecological processes on reefs. Yet given the limited-resolution of their Holocene record, it is uncertain how this will impact accretion and structural integrity over longer timescales. In addition, reports of this ecological decline have focused on intrinsic parameters such as coral cover and colony size at the expense of extrinsic ones such as geomorphic and environmental variables. Despite these problems, several attempts have been made to predict long-term accretion status of reefs based entirely on the contemporary health status of benthic communities. Here we explore how this ecological decline is represented within the reef geomorphic structure, which represents the long-term expression of reef development. Using a detailed geomorphic zonation scheme, we analyse the distribution and biodiversity of reef-building corals in fringing-reef systems of the Mesoamerican Reef tract. We find a depth-related pattern in community structure which shows that the relative species distribution between geomorphic zones is statistically different. Despite these differences, contemporary coral assemblages in all zones are dominated by the same group of pioneer generalist species. These findings imply that first, coral species distribution is still controlled by extrinsic processes that generate the geomorphic zonation; second, that coral biodiversity still reflects species zonation patterns reported by early studies; and third that dominance of pioneer species implies that modern coral assemblages are in a prolonged post-disturbance adjustment stage. In conclusion, any accurate assessment of the future viability of reefs requires a consideration of the geomorphic context or risk miscalculating the impact of ecological changes on long-term reef development.

INTRODUCTION

The declining cover of reef-building corals on modern reefs has become a global concern for both scientists and citizenry. The gravity of the situation became clear after only a decade of systematic monitoring, when a series of acute disease outbreaks decimated the dominant reef-building acroporid corals in the Caribbean (Knowlton et al., 1981; Gladfelter, 1982; Hughes, 1994; Aronson and Precht, 2001). Along with destruction caused by multiple strikes from intense hurricanes (e.g.,Woodley et al., 1981), these outbreaks were quickly followed by regional mass mortality of algal-grazing Diademid urchins, which resulted in macroalgal blooms (Lessios et al., 1984; Gladfelter, 1982; Lewis, 1984). By the 1990's acroporid reefs began suffering climate-induced mass-bleaching episodes and disease epidemics also began affecting other major reef-builders (orbicellids) that had survived previous disturbances (Eakin et al., 2010; Weil, 2004; Bruckner and Bruckner, 2006). These losses from disease and destruction were exacerbated by overfishing and nutrient pollution resulting from widespread and uncontrolled coastal development (Grigg and Dollar, 1990; Rogers and Beets, 2001; Hughes et al., 2003). By the turn of the century, surveys were reporting a regional decline in coral cover of more than 50 % across the Western-Atlantic Reef Province (Gardner et al., 2003; Schutte et al., 2010; Jackson et al., 2014; Cramer et al., 2020), producing a functional homogenization of coral species and a flattening of reef structure (e,g, Álvarez Filip et al., 2009; González-Barrios et al., 2021). Understanding of the extent of this decline on a regional scale, however, has relied exclusively on the data pooling from limited local observation, and this has led to significant uncertainty regarding its principal cause (Murdoch and Aronson, 1999; Wood, 2007; Jackson et al., 2014).

It is well understood that pooling ecological data from local studies can lead to inaccurate results, predict potential pseudo-trends, or misinterpret ecological processes because of scale changes in the analysis (Guzmán et al., 1991; Karlson and Hurd, 1993; Williams et al., 2015; Medina-Valmaseda et al., 2020; Dietzel et al., 2020). This is because regional meta-analyses extrapolate from small-scale coral abundance and coverage data gathered with different primary objectives in mind. A common problem, for example, is the relation between sampling scale and sensitivity of the observed ecological changes (e,g, Edmunds and Bruno, 1996), with extrapolation from small- to large-scale being performed without explicit sampling at new scales (Wiens, 1989). Furthermore, although regional meta-analyses account for inconsistencies among the various survey methods (Côté et al., 2005), they cannot account for inconsistencies resulting from omissions. The omission of the geomorphic context of ecological data by local studies, for example, can lead to inaccuracies in abundance-based data and thus misrepresent long-term spatial complexity and the ecological functioning of coral reefs at larger scales (e,g, Jackson et al., 2014; Williams et al., 2015; Medina-Valmaseda et al., 2020).

Although elucidating the role of abiotic factors in coral community structure is challenging because of these scale differences (Murdoch and Aronson, 1999), separating ecological data from its geomorphic context risks obscuring spatial trends (e,g, Williams et al., 2015). From an ecological perspective alone, the use of single ecological metrics, such as coral cover, to evaluate heterogeneous processes at regional scales gives an overly simplistic representation of reef structure (Viehman et al., 2009). A better understanding of the relationship between biotic data and its geomorphic context at larger scales, however, might be useful in interpreting the real signal of functional changes and improving long-term predictions of coral reefs and their response to global threats. Accretion potential, for example, has been reported to be heterogeneous among geomorphic zones (Perry, 1999; Blanchon et al., 2017) and also species-dependent (Perry and Alvarez-Filip, 2019; González-Barrios et al., 2021). This issue is relevant at larger temporal scales because not all coral species contribute equally to reef accretion (Macintyre and Glynn, 1976; Kuffner et al., 2019; Toth et al., 2019) and there are some biases and uncertainties in linking contemporary coral patterns with accretion potential (Wood, 2007).

Here we investigate whether geomorphically-controlled patterns in the decline of coral cover reported by Medina-Valmaseda et al. (2020) can be extended to the entire shallow geomorphic framework of the Mesoamerican reef tract. Using a standard geomorphic scheme and multi-year coral-cover and composition data, we analyze regional patterns in coral distribution and biodiversity. Then, using GIS-based environmental data, we explore how these patterns are influenced by key environmental controls on

92 reef geomorphology: depth, wave exposure and hurricane incidence. We find that contemporary coral
93 assemblages are dominated by the same group of pioneer species but that their distribution between
94 geomorphic depth zones is statistically different, and has not been completely homogenized by the decline
95 in reef condition over the last 50 years.

METHODS

Study region & geomorphic framework

98 The Mesoamerican Reef Tract (MART), located within the Western Caribbean marine ecoregion, stretches
99 ∼ 1000 kilometres along the coasts of the Yucatan peninsula and northeast sector of Central America
100 (Figure 1; Spalding et al., 2007). It is composed of shallow detached fringing reefs that consist of two main
101 geomorphic zones, a protected back-reef zone and an exposed reef-front zone separated by a crestline
102 where waves break. These breakwater structures are limited to shallow water (< 10 m deep) and are
103 developed over and adjacent to a bedrock terrace which is veneered by coral grounds (Rodríguez-Martínez
104 et al., 2011). Together the reef and terrace form a relatively consistent seascape over the inner fore-reef
105 shelf (< 15 m) throughout the Caribbean (Blanchon, 2011). The shallow geomorphic framework of the
106 MART is therefore consistent with the geomorphic zonation scheme first described from Grand Cayman
107 by Blanchon and Jones (1995) and later summarized by Blanchon (2011), who both used slope breaks
108 to identify reefal boundaries. We adopted this basic geomorphic scheme for all sectors of the MART
109 including both Belize and Honduras.
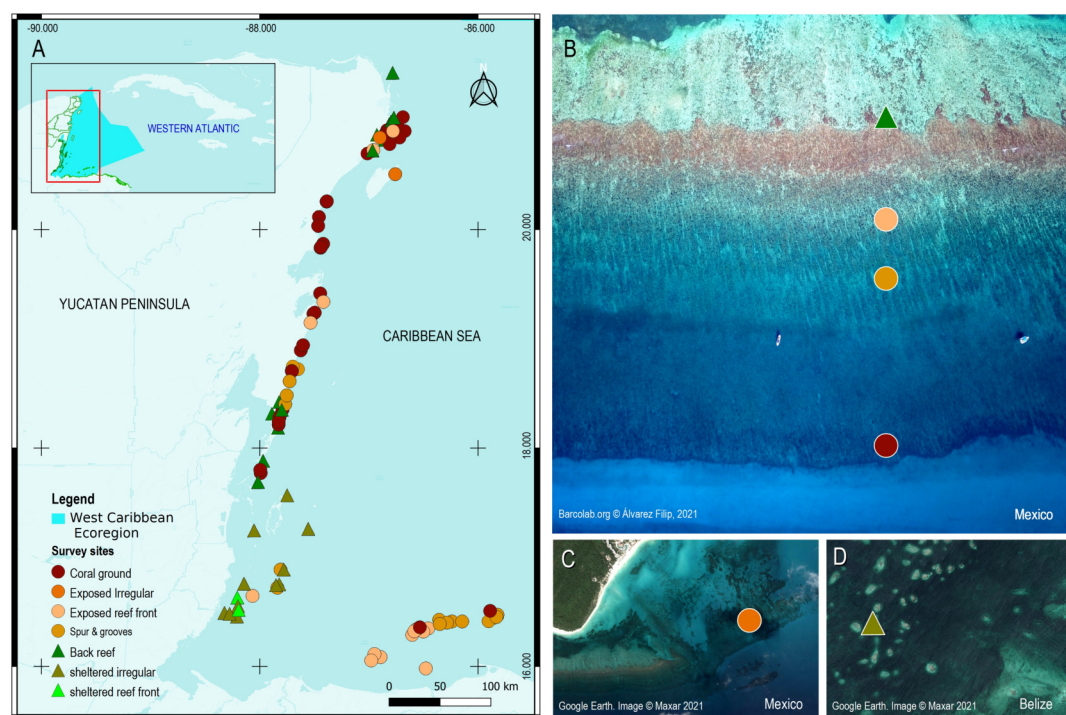
Figure 1. Survey sites and their geomorphic zones in the Mesoamerican reef tract (MART). Panel A. The MART is located in the West Caribbean ecoregion (represented by the irregular light blue polygon). Panel B, C, D. Reef sites are represented by colored symbols that correspond either to their benthic geomorphic zone and/or wave-energy designation. Map product was created with QGIS 3.14 Pi (QGIS Development Team, 2020)

110   In the northern Mexican sector of the MART, fringing reefs are relatively underdeveloped with

111 limited reef-fronts that only extend to a depth of $\sim 6 - 8$ m, thereby producing a more extensive bedrock
112 terrace veneered by coral grounds (Blanchon et al., 2017). The edge of this terrace is marked by a
113 slope break (mid-shelf break) and is commonly covered by a non-accretionary coral-ground community
114 (Rodríguez-Martínez et al., 2011). In the Belize sector, fringing reefs transition into better developed
115 Barriers and Atolls, and their reef-fronts extend into deeper water covering the bedrock terrace. At some
116 sites, reef-front subzones like the spur-and-groove can extend all the way to the shelf edge in 25-30 m of
117 water (James and Ginsburg, 1979; Burke, 1982). In the Honduras sector, reef development is restricted
118 to the offshore Bay Island group: Roatan, Utila, Guanaja, and Cayos Cochinos. These reefs also have
119 extensive spurs-and-grooves zones extending to the shelf edge (Almada-Villela et al., 2003).
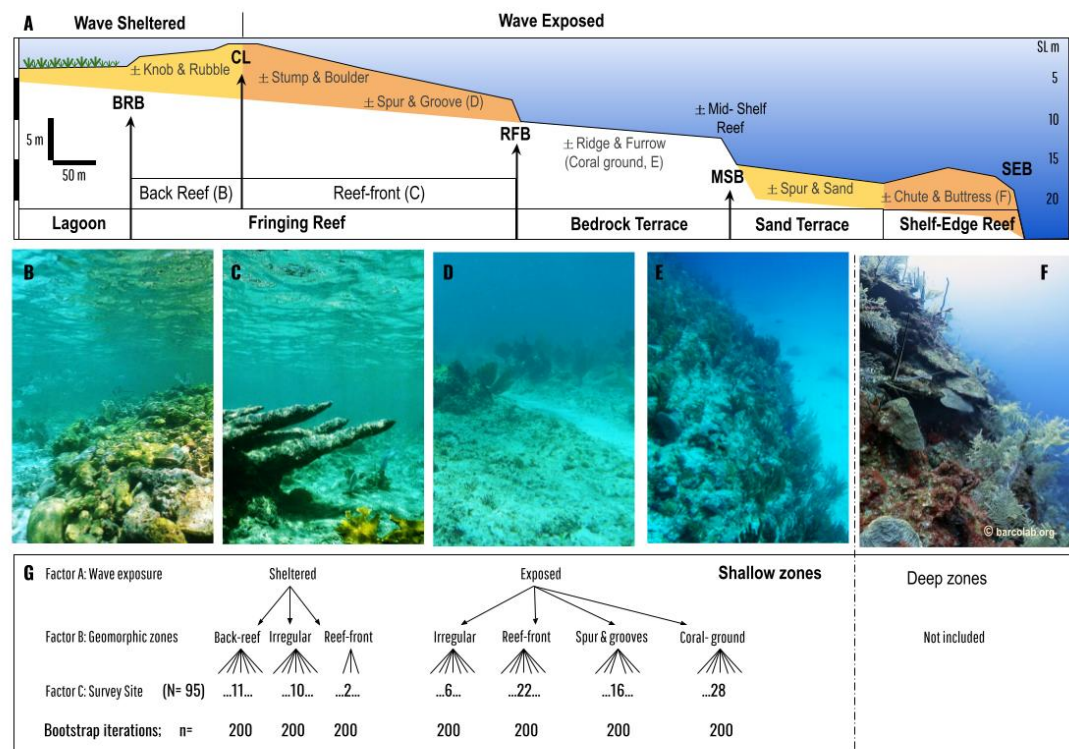
Figure 2. Geomorphic zonation of an idealized shelf showing shallow reef and benthic zones typical of
Mesoamerican reef seascapes (following Blanchon et al., 2017. Zones are delineated by slope breaks:
Back-Reef break (BRB), Crestline (CL), Reef-Front break (RFB), Mid-Shelf break (MSB), and
Shelf-Edge break (SEB). Main benthic zones in bold are divided into wave sheltered (such as lagoon and
back-reef) and wave exposed (such as reef-front, bedrock terrace, sand terrace etc) (see Blanchon and
Jones (1995) for their descriptions). Each benthic zone can be divided into sub-zones that may or maynot
be present (±). Coloured zones are depositional or accretionary (like the fringing reef, or shelf-edge reef)
whereas non-coloured are erosional or non-accretionary (like the bedrock terrace with its superficial coral
ground). Our analysis is restricted to coral communities covering the fringing reef and the adjacent
bedrock terrace (coral ground). Panels B, C, D, E and F give an overview of these coral communities:
Back Reef (B), Reef Front (C), Spur & Groove (D), Coral-ground, and mid-shelf reef (E), and Shelf-Edge
reef (F, which is not included in the study). Panel G is a schematic of the asymmetrical design for
PERMANOVA analysis, encompassing three factors (wave exposure, geomorphic zones and survey site)
with different levels of nested factors (back reef, reef front, irregular etc) encompassed by 2 upper levels
(sheltered and exposed)

120 We follow the geomorphic scheme of Blanchon (2011) to classify all sites based on retrospective
121 satellite imagery from virtual globes such as Google Earth and ArcGIS online. A small number of sites

122 ($\sim 2\%$) had unclear images due to cloud cover and/or sea state, and geomorphic zoning was more difficult
123 to delineate at the subzone level (for example, defining the boundary between the spur and grooves
124 reef and non-tree bedrock terrace). In these few cases, we classify the sites as the most common type
125 for that depth and zone based on field experience and expert consultation. Sites where reefs are less
126 organized ($\sim 17\%$) and lack a clear geomorphic structure, are simply classified as undifferentiated zones
127 and assigned as either protected or exposed wave environments. Although uncommon, some of these
128 'exposed' zones can be found in semi-sheltered sites with complex coastal geography, (e.g. the barrier
129 reef fronts behind offshore atolls in the Belize sector).

Coral distribution in geomorphic zones

131 To document the spatial distribution of scleractinian coral within shallow geomorphic zones we use
132 information from two databases, the Caribbean Reef Information System (CRIS, Barcolab.org) and
133 the Healthy Reefs Initiative (www.healthyreefs.org), which contain data on coral cover es-
134 timates at site level. Data in these sources come from published literature, research projects, and
135 monitoring programs. In all cases, coral cover information was obtained using two similar benthic
136 survey methodologies (Line Intercept Transect- LIT and Point Intercept Transect-PIT) according to
137 Atlantic and Gulf Rapid Reef Assessment Benthic Protocol (AGRAA, Lang et al., 2012) available at
138 https://www.agrra.org/coral-reef-monitoring) and the Mesoamerican Barrier Reef
139 System monitoring program (Almada-Villela et al., 2003). Each survey includes between six and ten
140 transects (10 or 30 m in length) haphazardly deployed at the reef sites. From these databases we select
141 only the most recent data from sites in a 1-10 m depth range that contain coral cover estimates at species
142 level. After discarding sites outside these requirements (e.g., depth range, data quality at species level),
143 we compile a subset of coral coverage from 95 survey sites between 2016 and 2018 (Table 1)

144 Based on this subset, we calculate the (i) overall site coral-cover data and (ii) the relative coral
145 cover of each species (i.e. the relative contribution of each species to the total coral cover). To avoid
146 potential confusion stemming from using the term coral cover to refer to the relative coral cover of each
147 species hereafter we refer to the latter as coral species contribution. Because of our interest in analyzing
148 spatial patterns within the geomorphic framework, coral-cover data are pooled and analyzed according to
149 geomorphic zone, and not survey site. Therefore, we compare overall coral-cover data of multiple sites
150 as a comparative sampling unit, for example, pooling coral-cover from all back-reef sites (Figure 2B).
151 The time period of data is chosen to avoid potential bias caused by the recent outbreak of the Stony Coral
152 Tissue Loss Disease (SCTLD) reported in the Mexican sector during 2018 (Alvarez-Filip et al., 2019).

Statistical analysis

154 Derivatives of abundance usually violate the assumptions of traditional parametric statistics, which makes
155 it difficult to deal with using traditional univariate methods (Fieberg et al., 2009). Therefore we use a
156 multivariate analysis which is effective in dealing with those data (Beals, 1984; Fieberg et al., 2020). This
157 type of analysis requires data to be transformed to reduce the differential between the largest and smallest
158 non-zero value in the transformed matrix (Clarke and Gorley, 2015). For the comparative analysis based
159 on the overall coral cover of each site, we use raw data, which is a standard procedure in ecological
160 analysis. But for the analysis of coral-community contribution to relative cover, although optional, a
161 pre-treatment of data standardization is made to reduce the differences in magnitude generated by the
162 disparate benthic methods and to reduce method-bias related to the effect of the former benthic scheme
163 that included other benthic classes (Vallès et al., 2019). In both analyses for the multivariate pre-treatment,
164 we choose a medium level (square-root) of data transformation. Further transformation is followed
165 by an ordination process where we construct the correspondent Bray-Curtis matrix of similarities. All
166 subsequent multivariate statistical analyses and graphical outputs are performed and constructed using
167 Plymouth Routines in Multivariate Ecological Research (Primer-e version 7.0.13, serial number 4901,
168 Clarke and Gorley, 2015).

169 To compare overall coral cover and related coral species contribution to relative cover of the com-

munities between geomorphic zones, we conduct asymmetrical analyses of permutational variance (PERMANOVA) at both levels of aggregation for factor 'site' (nested within the geomorphic zones by wave exposure) and nested in wave exposure regimes on the basis of Bray-Curtis similarity measures of transformed square-root matrix of ecological data (Anderson, 2006). Including these permutations, procedures offer an alternative to Normal-based inferential methods as they are adaptable and require fewer assumptions, whereas the asymmetrical design deals with a different number of geomorphic zones by wave exposure, three sheltered and four exposed. The experimental design consisted of 3 factors (Figure 2.C): Factor A: wave exposure (fixed with a = 2 levels: sheltered and exposed), Factor B: Geomorphic zones (fixed, nested in wave exposure with 3 levels nested in sheltered, and 4 levels nested in exposed), and Factor C: Site (random, nested in geomorphic zones, wave exposure) with 95 levels. The test uses permutation of residuals under a reduced model and Type III (partial Square Sums) in 9999 permutations.

To test the homogeneity of multivariate data dispersion in each case, we performed a non-parametric permutational analysis of multivariate dispersion (PERMDISP), along with pairwise comparisons of the Bray-Curtis matrix of similarities. PERMDISP is performed based on distances to centroids, with P-values (p(perm)) obtained from 9999 permutations, giving the best overall results expected in terms of type I error and power (Anderson et al., 2006). To determine the species contributions to coral cover within each geomorphic zone we conduct a two-way similarity percentage analysis (SIMPER) for zones by wave exposure, based on Bray-Curtis similarity measures of transformed square-root matrix of abundance data, making a 70 % cut-off for low contributions (Clarke and Warwick, 1994; Clarke et al., 2014a). We present the results through the metric MDS of bootstrapped averages for 95 % region estimates. Bootstrap averages test iteratively resamples each group by its geomorphic zone type 200 times creating a plot of 4m dimensions multivariate effect. Such a bootstraps procedure allows better visualization of how the mean response of each data group varies with changes in predictor values if we were to collect another sample of observations from a different set of geomorphic zones (Fieberg et al., 2009). The arrangement of the number of sites by its geomorphic zone classification lacks sampling balance (Figure 2B) and therefore, another advantage of this approach is its success in estimating parameters of a statistical distribution for a balanced number of copies from our data whereas preserving the original structure of its data set (Fieberg et al., 2020).

Extrinsic factors

For the purposes of this study, we consider extrinsic factors to be the diverse environmental variables that describe the abiotic context of coral communities including physicochemical variables and non-biotic disturbances, such as depth gradient, wave exposure and hurricane impacts. To evaluate the response of the biotic multivariate data to its corresponding multivariate environmental data we select information from both benthic surveys and cyclonic disturbances available for the MART. We use depth of benthic surveys and environmental information extracted from the open-source Physical Environments of the Caribbean Sea classification of Chollett et al. (2012) as geographic information system layers. For this, we extract data of physical disturbances including exposure to wind- and tropical-storm waves and the number of hurricane impacts using the QGIS (v. 3.14 Pi) Point Sampling Tool plugin, v.0.5.3 available at https://github.com/borysiasty/pointsamplingtool. Where the plugin failed because of no-value pixels, we manually selected the neighbouring major value. Furthermore, we check the distribution of all environmental variables for skewness and outliers and log-transform all data except the depth of each sampling site (following Clarke and Gorley, 2006). Finally, we normalize data to place each variable on the same dimensionless scale (for example, Clarke et al., 2014b). Environmental data are graphically represented through a Principal Coordinate Analysis (PCO) where vectors are the raw Pearson correlations of variables with the Principal Component Analysis (PCA) values (Torgerson, 1958; Gower, 1966).

To analyze and generate an exploratory hypothesis model on the spatial relationship between multivariate data clouds of the biotic response variables (coral species distribution) and that of regional environmental gradients, we test a distance-based linear model (DISTLM, Legendre and Anderson, 1999). The DISTLM test includes the Bray-Curtis matrices of previously square transformed data of coral species distribution and logarithm Euclidean distance-based matrix of previously normalized environmental

data in 9999 permutations within the factor Geomorphic zone for the environment. The test assumes
non-linearity and additivity of the abiotic variables on the high-d community response. To visualize fitting
models in multi-dimensional space we use the distance-based redundancy analysis (dbRDA, Legendre and
Anderson, 1999; McArdle and Anderson, 2001) based on the Euclidean-distance matrix of environmental
data.

RESULTS

Coral cover patterns in geomorphic zones

A total of 95 survey sites with 50 from Mexico, 25 from Belize and 20 sites from Honduras are included in
this study. Sites encompass seven different types of geomorphic zones and subzones in both wave-exposed
and protected environments along the regional latitudinal gradient. The result of the PERMANOVA test
indicates that there are no significant differences in LCC between wave sheltered and wave-exposed
geomorphic zones (P(perm)= 0.39; Figure 3A; *Data S1*), although when species identity is included in the
relative composition analysis, there are significant differences between geomorphic zones (Fig. 3B). The
asymmetrical PERMANOVA test including the three terms 'wave exposure', 'Geo zone (wave exposure)'
and 'site (Geo zone (wave exposure))' results in a statistically significant P(perm) and P(MC) < 0.01,
(Fig.3A; Data S2).
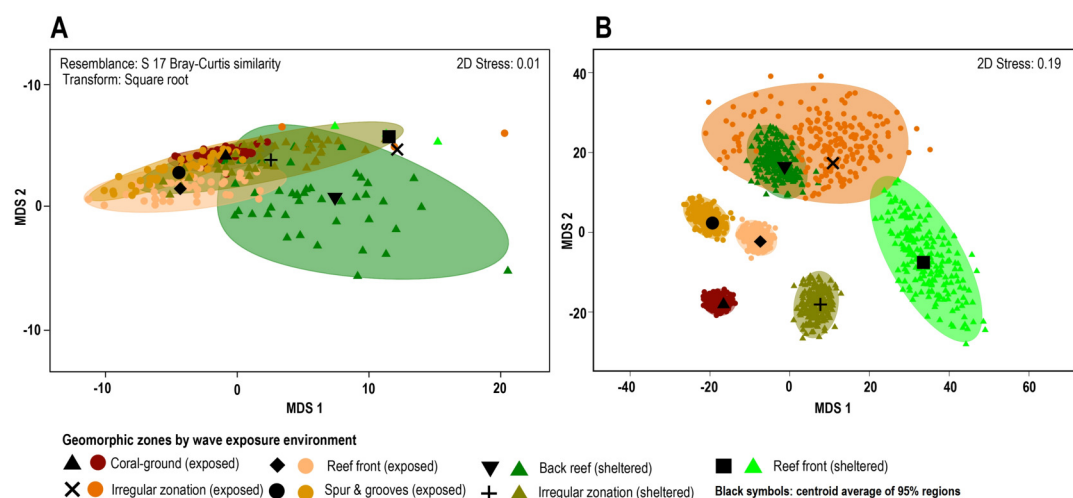
Figure 3. Coral cover patterns by geomorphic zone. Panel A shows the similitude of overall coral cover
for each geomorphic zone type and wave exposure through a metric MDS of 'whole sample' bootstrap
averages resampling the n-transects of each sampling site 200 times (arranged by geomorphic zones and
wave environment). nMDS shows the approximate 95% region estimates fitted to the bootstrap averages
and the relative estimated position of centroids for each group (symbols in black, Figure 3A, B). Panel B
shows Species contribution to the relative cover within each geomorphic zone. The contribution of coral
species to each geomorphic zone clearly represents long-term spatial patterns and highlights the absence
of real species homogenization through the reef seascape (3D stress: 0.08).

237   The estimates of components of variation (S) for the three orthogonal factors were wave exposure:
238 178.52; Geo zone nested in wave exposure: 214.98; and site nested in Geo zone nested in wave exposure:
239 875.33. The site factor, therefore, contributes most to differences in species contribution, followed by the
240 geomorphic zone, with wave exposure having the least control. A posteriori pairwise PERMDISP test at
241 the LCC level shows homogeneity of variance in all groups (F: 1.49, df1: 6, df2: 84; p(perm): 0.3422;
242 *Data S3*), whereas the species contribution level shows heterogeneity in data variance involving pairwise
243 tests for single or combined irregular and exposed zones (F: 13.23, df1: 6, df2: 543; p(perm): < 0.01;
244 *Data S4*). Other cases, including the irregular and combined sheltered/exposed geomorphic zones, show
245 homogeneity in data variances (F: 13.23, df1: 6, df2: 543; p(perm):< 0.01; Figure 3B). In total 61% of
246 possible pairwise tests show homogeneity in data variance and do not show a particular trend under the
247 current PERMANOVA design. These tests indicate that there are differences in coral-species distribution
248 between geomorphic zones (PERMANOVA), and in the variance of data distribution (PERMDISP) in
249 several geomorphic zones within the same environments (Fig. 3, *Data S4*).

250   The contribution of individual species to observed differences is assessed using the SIMPER test
251 (*Data S5*. Results show that in exposed geomorphic zones three species overlap: *Agaricia agaricites,*
252 *Porites astreoides* and *Siderastrea siderea* (Average similarity: 30.0) with relative contributions of 32.2 %,
253 24.3 % and 15.1% respectively. In sheltered zones another trio of species overlap, *P. astreoides, Orbicella*
254 *annularis* and *Agaricia agaricites*, (Average similarity 25.7) with relative contributions of 49.0 %, 18.5
255 % and 8.4 % respectively (Data S). Interestingly, an almost identical group of species accounts for the
256 81.2 % average dissimilarity between samples. In terms of dissimilarity, only four species (*S. siderea,*
257 *Porites astreoides, O. annularis* and *A. agaricites*) which contribute ~ 10 %, form roughly 53 % of the
258 differences between samples. Overall, across all wave exposure zones, the largest average similarity of
259 34.9 % corresponds to the exposed Coral-ground zone, and the lowest 18.2 % to the sheltered Back-reef
260 zone.

261 **Coral species patterns and extrinsic factors**

262 Average species richness (number of species identified to lowest possible taxonomic level; S) increase
263 with the depth being the lowest in sheltered back- reef (2.1) whereas the deeper coral- ground zone exhibit
264 the highest value (4.9). Also species diversity as measured by the Shannon– Weiner index (H´) follows
265 the same pattern increasing seaward from the back- reef (0.9) towards coral-ground zone (1.4; Table 1).

266   On a regional scale, all sites are exposed to similar wave-exposure regimes regardless of geomorphic
267 zone, whereas hurricane impact varies between sites (Figure 4). When analyzed by geomorphic zone
268 and wave exposure, the average depth of sites varies from 1.8 ± 2.9 m in sheltered reef-front zones,
269 to 11.2 ± 4.2 m in exposed coral-ground zones. Chronic stress derived from wave-exposure for these
270 sites varies between 5.9 ± 0.9 and 7.4 ± 0.2 J m $^{-3}$. Whereas acute mechanical stress derived from
271 hurricane frequency in the last 157 years (1851–2008) varies between 11 ± 2 y and 20 ± 2.8 yr (Table 1).
272 Regional patterns of three selected environmental data are presented in the Principal Coordinates Analysis
273 (PCO) of Figure 4. It shows that the first two axes explain 81.6 % of the internal variability of these three
274 environmental variables, indicating that the 2-d ordination is likely to have captured the majority of the
275 patterns of multidimensional data variation. Accordingly, the depth of the reef site and hurricane impact
276 explain 42.2 % of variations of the PCO1 axis, whereas wave energy exposure alone explains roughly
277 the same percentage (39.5 %) of the PCO2 axis. In addition, depth and hurricane impact appear to act
278 inversely over coral species patterns (Figure 4A).

Geomorphic zone	S ± SD	H´(av.) ± SD	D ± SD	WE* ± SD	HO* ± SD
Reef Front_sheltered	2.1 ± 1.2	0.5 ± 0.5	1.8 ± 2.9	5.9 ± 0.9	14 ± 2.1
Back Reef_sheltered	3.8 ± 2.0	1.0 ± 0.5	2.8± 2.9	7.5 ± 0.1	18 ± 4.7
Irregular_sheleted	3.8 ± 2.0	1.0 ± 0.5	2.9± 2.6	6.3 ± 1.4	11 ± 2.0
Irregular_exposed	3.8 ± 2.0	1.0 ± 0.5	3.7± 1.8	7.6 ± 0.1	20 ± 2.8
Reef Front_exposed	3.8 ± 2.0	1.0 ± 0.5	5.9± 2.5	7.1 ± 0.8	12 ± 5.4
Spur &Grooves_exposed	3.9 ± 2.0	1.0 ± 0.5	6.5± 2.5	7.3 ± 0.5	12 ± 1.1
Coral Ground_exposed	3.9 ± 2.0	1.0 ± 0.5	11.2± 4.2	7.4 ± 0.2	12 ± 4.7

Table 1. Species richness (S), Diversity (H´) and abiotic factors (D, WE, HO) by geomorphic zone and environmental exposure. Abiotic factors correspond to physical environments of the Caribbean Sea stratification scheme of mechanical disturbances acting over coral communities at the surveyed reef sites. These include both chronic disturbances from wind-driven wave exposure and acute disturbance after Chollett et al. (2012). Chronic stress, given by wave exposure (WE), is related to wind conditions between 1999–2008 for the entire basin, whereas acute stress is given by the frequency of occurrence of hurricanes (HO) with Category 1–5 magnitudes in the last 157 yr (1851–2008). Values of mechanical disturbances (*) are extracted from geographic information layers. D: average depth in meters, WE: Wave exposure in J m $^{-3}$, HO: hurricane occurrence in number of events, SD: standard deviation.
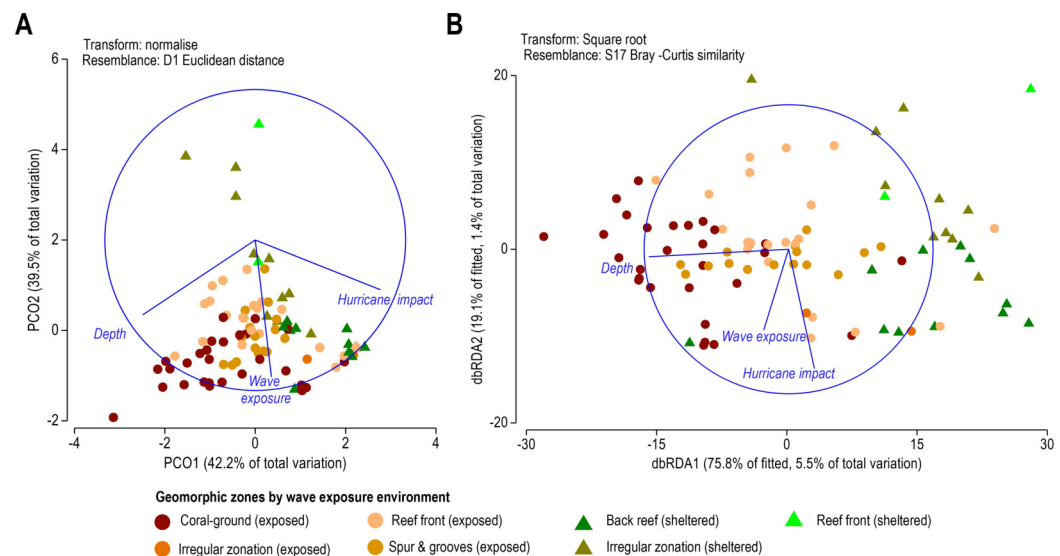
Figure 4. Panel A. Principal Coordinates Analysis (PCO) shows the multivariate environmental data cloud of three selected variables. Note the first two axes explain 81.6 % of the internal variability of these three environmental variables with depth having a contrasting effect with hurricane depth and wave exposure acting differently. Panel B. Distance-based Redundancy Analysis (db-RDA) graphically illustrates the Distance-based linear model (DISTLM) results. It shows correlation trends between the Bray-Curtis distance matrix of biotic response and the explanatory Euclidean distance matrix of environmental variables.

279 Results from the DISTLM marginal tests (Data S6) show how much can be explained by each abiotic
280 variable alone, ignoring other variables. Tests show that the depth of reef sites exert the highest influence
281 explaining 5.5 % of the overall variability in coral species contribution (p < 0.01, Data S4A, Fig. 4B).
282 Wave exposure and the number of major hurricane impacts when each is considered alone explain roughly
283 1 to 1.5 % (p < 0.01, Data S4A, Fig.4B) of variability in species contribution to each geomorphic zone.
284 These results indicate that spatial patterns in coral species contribution by geomorphic zones are still
285 responsive to these three environmental variables.

DISCUSSION

287 Our findings confirm the decline in acroporids on Mesoamerican reefs and the shift to an alternate 'weedy'
288 state but show that this has not yielded a complete homogenization of the coral community. Although
289 data analysis shows that the overall cover of corals is similar between geomorphic zones, species patterns
290 within them are statistically different. All zones are dominated by the same community of generalist
291 species (*Agaricia and Porites*), but these are distributed differently in space. In exposed zones, *Agaricia*
292 *agaricites* makes the largest contribution followed by *P. astreoides* and *Siderastrea siderea*, whereas in
293 sheltered zones *Porites astreoides* dominates followed by *Orbicella annularis* and *A. agaricites*. The
294 species responsible for differences between zones are *S. siderea, P. astreoides* and *O. annularis*. These
295 differences confirm that extrinsic factors such as wave and hurricane exposure still have an impact on
296 species distribution patterns, despite the large historical decline in coral cover.

297 We recognise that these extrinsic factors generate a weak signal in the degraded coral community
298 and this is likely impacted by the methodological protocol. For example, only a limited number of
299 long-term variables were considered in analysing the species distribution patterns and, two of these (waves
300 and hurricanes), exhibit significant variability over short temporal scales. Nevertheless, both have been
301 reported as major environmental drivers of ecological processes including species zonation (Geister, 1977;
302 Hughes et al., 2019). Moreover, the impact of such disturbances creates an adaptive biotic response by
303 influencing the life-history traits of coral assemblages and creating scale-dependent patterns of species
304 distribution, with some being better adapted to hurricane impacts (e.g, Chollett and Mumby, 2012). In
305 addition, the result is also consistent with multiple reports of the increasingly important role that tropical
306 cyclones play in shaping coral reef ecosystems at both short- and long-term scales (Blanchon et al., 1997;
307 Lugo et al., 2000; Blanchon et al., 2017; Hogan et al., 2020; Puotinen et al., 2020). Moreover, several
308 schemes have proposed an adaptive response of coral assemblages to wave exposure regimes (e.g, Adey
309 and Burke, 1977; Geister, 1977). To some extent, our results augment these schemes by assigning a
310 geomorphic framework and providing an alternative approach to imprecisely defined species-zonation
311 limits. However, wave-fetch becomes saturated on a regional scale and its role in these schemes has
312 been questioned (Adey, 1978). If this is accurate then it could help explain the linkage weakness in
313 Mesoamerican reefs.

314 The replacement of former acroporid-dominated zones by modern generalist assemblages may result
315 from a species succession associated with hurricane disturbance, where an initial post-hurricane adjustment
316 stage is combined with the loss of species redundancy (McWilliam et al., 2018). Generalist assemblages
317 are formed by pioneer species which are considered to be adapted to repeated disturbance but controlled
318 by depth-related parameters. The evolutionary success of *P. astreoides*, for example, is supported by its
319 limited longevity and its weedy life-history strategy which allows it to thrive in a wide variety of shallow
320 habitats (Tomascik and Sander, 1987). In addition, pioneer assemblages that remain after disturbances are
321 vestigial, given the large historical reductions in absolute abundance (which has dropped ∼ 50 %) and
322 loss in species redundancy (leaving only generalists). Consequently, some weakness is expected in the
323 biotic-environmental signal and, with these data, it is not possible to rule-out a successional community
324 status (González-Barrios et al., 2021). The environmental variables may also act as a proxy for other
325 unknown variables influencing coral assemblages (Ellis et al., 2019; Hughes et al., 2019).

326 The impact of reef geomorphology on coral species composition has been largely ignored in both
327 original (local) and regional analyses (e.g., Rioja-Nieto and Álvarez-Filip, 2019; Contreras-Silva et al.,

2020; Estrada-Saldívar et al., 2019. In the case of local studies, that omission has less impact given that the environment is more homogeneous (but see Medina-Valmaseda et al., 2020), but becomes a problem at a regional scale as environment heterogeneity increases. Furthermore, many local studies pooled data from combined geomorphic zones such as the 'fore-reef' which lump non-accreting zones from the surrounding seascape with accretionary reef zones (Williams et al., 2015; Medina-Valmaseda et al., 2020). By providing a more accurate geomorphology our results clearly show a pattern of depth-related geomorphic control down the entire Mesoamerican reef tract, implying that the geomorphic framework is a long-term result of the feedback between environmental processes and coral communities. A similar finding from another site in the region has been reported by Medina-Valmaseda et al. (2020) who found that the inclusion of geomorphic zones in factor-analysis helped identify differences in coral species distribution patterns. Together, these findings underline the importance of depth-related geomorphic controls on large-scale coral-species patterns. Indeed, it is remarkable that geomorphic control prevails on coral communities despite the long duration over which reef decline has occurred.

Geomorphic context was indirectly addressed by a recent province-wide meta-analysis Jackson et al. (2014), which highlighted the significance of reef environment and depth amongst others. The resulting trends, however, are still based on pooling of local data, and thereby relegate the role of environmental factors. Perhaps this lack of consideration of geomorphic context in ecological studies is a methodological artifact whereby reef environment and geomorphic context are relegated to the study site section. Regardless of the cause, the use of a detailed geomorphic zonation within any ecological analysis facilitates the consideration of extrinsic long-term factors. It also provides long-term accretion boundaries to benthic communities and thus incorporates geological models of reef development which are an important source of information on spatial and temporal heterogeneity of the seascape. As a consequence, although ecological studies provide a detailed snapshot of recent changes in coral communities, without a precise geomorphic context, they risk providing an inaccurate picture of both ecological and long-term reef development (Aronson and Precht, 1997; Bellwood et al., 2004; Bruckner, 2012).

CONCLUSIONS

Despite a large decline in historical cover, the depauperate coral communities on fringing reefs of the Mesoamerican Reef Tract still show species-level differences between depth-related geomorphic zones. These spatial differences, however, are subtle and have been missed by previous ecological surveys, which have claimed that communities are homogenized and therefore represent an unnatural alternative state and compromise the accretion potential of future reef development. Although the decline of acroporid framebuilders has resulted in a partial homogenization between zones, it is still uncertain if the new 'pioneer state' is stable on the long timescales over which reef accretion occurs. Moreover, species-level differences in the distribution of pioneer species between geomorphic zones may be a response to their adaptive life-history traits after prolonged disturbance. The fact that these species are early colonizers therefore points towards a post-disturbance adjustment and implies that this community may result from a successional failure induced by chronic anthropogenic disturbance (related to mass tourism along the Mayan Riviera). But the health status of local communities can vary on short-term scales and adapt to fluctuations in disturbances.

We conclude that an accurate analysis of spatial ecological trends in coral reefs requires a detailed geomorphic framework in order to identify subtle changes in communities at large spatial scales. If a geomorphic context is not provided, then a random selection of coral sites will under-represent the complexity in species patterns. Consequently, we suggest that including a geomorphic context is a fundamental prerequisite for accurately determining the signal of ecological changes on local, regional, and provincial scales. Finally, our results do not exclude the possibility of similar heterogeneous patterns in coral communities at other levels of organization, such as reef type.

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