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

Alexis Enrique Medina-Valmaseda[1,2], Paul Blanchon[2], Lorenzo Alvarez-Filip[3] and Esmeralda Pérez-Cervantes[3]

[1] Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, Mexico
[2] Reef Geoscience Group, Unidad Académica de Sistemas Arrecifales Instituto de Ciencias de Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico
[3] Biodiversity and Reef Conservation Laboratory, Unidad Académica de Sistemas Arrecifales Instituto de Ciencias de Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico

ABSTRACT

The development of coral reefs results from the 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 the 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 analyze 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 risks 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 & 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 1990s 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 (*Muller et al., 2010*; *Weil, 2004*; *Bruckner & Bruckner, 2006*). These losses from disease and destruction were exacerbated by overfishing and nutrient pollution resulting from widespread and uncontrolled coastal development (*Grigg & Dollar, 1990*; *Rogers & 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, Selig & Bruno, 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, Cabral-Tena & Alvarez-Filip, 2021*). Understanding 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 & 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, Jackson & Weil, 1991*; *Karlson & Hurd, 1993*; *Williams et al., 2015b*; *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 & 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., 2015b*; *Medina-Valmaseda et al., 2020*).

Although elucidating the role of abiotic factors in coral community structure is challenging because of these scale differences (*Murdoch & Aronson, 1999*), separating ecological data from its geomorphic context risks obscuring spatial trends (*e.g., Williams et al., 2015b*). 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, Thur & Piniak, 2009*; *Hughes et al., 2010*; *Kuffner & Toth, 2016*). 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 & Alvarez-Filip, 2019*; *González-Barrios, Cabral-Tena & Alvarez-Filip, 2021*). This issue is relevant at larger temporal scales because not all coral species contribute equally to reef accretion (cf. *Macintyre & 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*).

Similarly, the use of the geomorphic zones to contextualize ecological indexes within restoration efforts might improve the outcome and enhance economic efficiency. Restoration efforts, for example, commonly lack geomorphological framework analysis in species distribution and omit the role of large-scale extrinsic factors, such as exposure to wave energy and reef degradation state. Such factors have been highlighted as the cause of restoration failures, in spite of the results being evaluated solely based on live coral coverage (*Hein et al., 2020*). To place this in context, it is estimated that the cost of Caribbean restoration programs varies between USD 10,000 ha^{-1} for the simplest transplant efforts and more than USD 2.0–6.5 million ha^{-1} in more complex projects involving the physical restoration of the reef framework (*Spurgeon, 2001*; *Edwards, 2010*) with a mean cost around USD 400,000 ha^{-1} (2010 USD; *Bayraktarov et al., 2019*). Given its variable history of success, the economic investment appears to be excessive in comparison to the modest results achieved in coral survival (~60%), duration (1–2 years) and extent (0.01 ha or 108 m^2; *Bayraktarov et al., 2019*).

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 reef geomorphology: depth, wave exposure and hurricane incidence. We find that contemporary coral assemblages are dominated by the same group of pioneer species, but that their distribution between geomorphic depth zones is statistically different, and has not been completely homogenized by the decline in reef condition over the last 50 years.
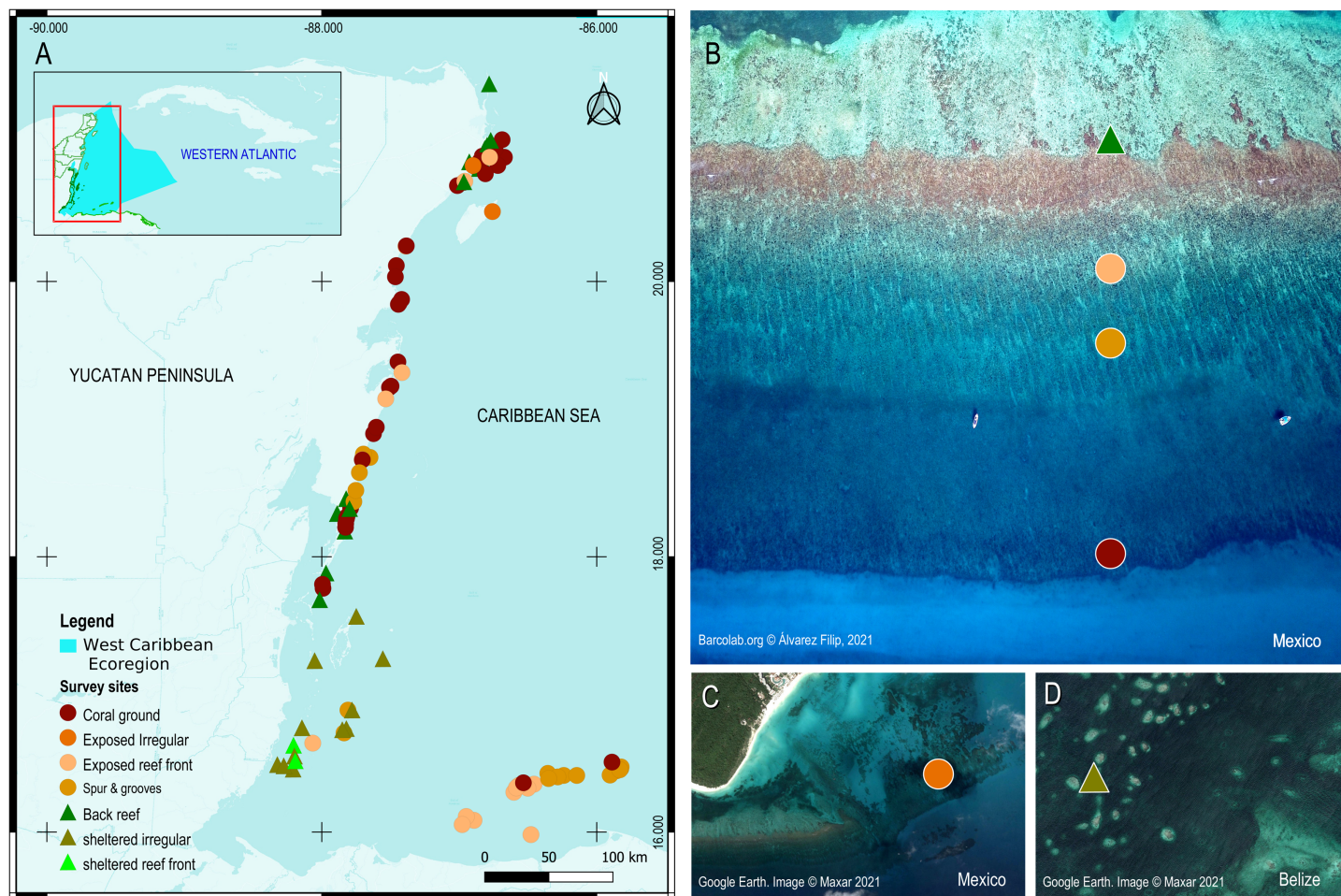
Figure 1 Survey sites and their geomorphic zones in the Mesoamerican reef tract (MART). (A) The MART is located in the West Caribbean ecoregion (represented by the irregular light blue polygon in the inset). (B–D) Reef sites are represented by colored symbols that correspond either to their benthic geomorphic zone and/or wave-energy designation. Map product was created with QGIS 3.14 Pi (*QGIS Development Team, 2020*).
Full-size ◩ DOI: 10.7717/peerj.12590/fig-1

METHODS

Study region and geomorphic framework

The Mesoamerican Reef Tract (MART), located within the Western Caribbean marine ecoregion, stretches ~1,000 km along the coasts of the Yucatan peninsula and northeast sector of Central America (Fig. 1; *Spalding et al., 2007*). It is composed of shallow detached fringing reefs that consist of two main geomorphic zones, a protected back-reef zone and an exposed reef-front zone separated by a crestline where waves break. These breakwater structures are limited to shallow water (<10 m deep) and are developed over and adjacent to a bedrock terrace which is veneered by coral grounds (*Rodríguez-Martínez et al., 2011*). Together the reef and terrace form a relatively consistent seascape over the inner fore-reef shelf (<15 m) throughout the MART (*Blanchon et al., 2017*). The shallow geomorphic framework of the MART is therefore consistent with the geomorphic zonation scheme first described from Grand Cayman by *Blanchon & Jones*

(1995) and later summarized by *Blanchon (2011)*, who both used slope breaks to identify reefal boundaries. We adopted this basic geomorphic scheme for all sectors of the MART including both Belize and Honduras.

In the northern Mexican sector of the MART, fringing reefs are relatively underdeveloped with limited reef-fronts that only extend to a depth of ∼6–8 m, thereby producing a more extensive bedrock terrace veneered by coral grounds (*Blanchon et al., 2017*). The edge of this terrace is marked by a slope break (mid-shelf break) and is commonly covered by a non-accretionary coral-ground community (*Rodríguez-Martínez et al., 2011*). In the Belize sector, fringing reefs transition into better developed Barriers and Atolls, and their reef-fronts extend into deeper water covering the bedrock terrace. At some sites, reef-front subzones like the spur-and-groove can extend all the way to the shelf edge in 25–30 m of water (*James & Ginsburg, 1979*; *Burke, 1982*). In the Honduras sector, reef development is restricted to the offshore Bay Island group: Roatan, Utila, Guanaja, and Cayos Cochinos. These reefs also have extensive spurs-and-grooves zones extending to the shelf edge (*Almada-Villela et al., 2003*).

Following the geomorphic scheme of *Blanchon (2011)* we classify all sites based on retrospective satellite imagery from virtual globes such as Google Earth and ArcGIS online. A small number of sites (∼2%) have unclear images due to cloud cover and/or sea state, and geomorphic zoning is more difficult to delineate at the subzone level (for example, defining the boundary between the spur-and-grooves and non-tree bedrock terrace). In these few cases, we classify the sites as the most common type for that depth and zone based on field experience and expert opinion. Sites where reefs are less organized (∼17%) and lack a clear geomorphic structure, are simply classified as undifferentiated zones and assigned as either protected or exposed wave environments. Although uncommon, some of these 'exposed' zones can be found in semi-sheltered sites with complex coastal geography (*e.g.*, the barrier reef fronts behind offshore atolls in the Belize sector).

Coral distribution in geomorphic zones

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

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 disturbances (*Chollett et al., 2012*). Chronic stress, given by wave exposure (WE), is related to wind conditions between 1999 and 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 years (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.

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

to avoid potential bias caused by the recent outbreak of the Stony Coral Tissue Loss Disease reported in the Mexican sector during 2018 (*Alvarez-Filip et al., 2019*).

Based on this subset, we calculate (i) the overall site live coral-cover data (LCC) and (ii) the relative coral cover of each species (*i.e.* the relative contribution of each species to the total coral cover). To avoid potential confusion stemming from using the term 'coral cover' to refer to the relative coral cover of each species, hereafter we refer to the latter as 'coral species contribution'. In ecological studies, this is referred to as the sites taxonomic β-diversity and can be partitioned into two components: one reflecting species replacement between communities (turnover) and other reflecting the difference in the number of species among communities (nestedness-resultant; *Baselga, 2012*). However, coral-cover data are pooled and analyzed according to their geomorphic zonation, and not survey sites. Therefore, we compare overall coral-cover data of multiple sites as a comparative sampling unit, for example, pooling coral-cover from all back-reef sites (Fig. 2B). The qualitative β-diversity analysis entails partitioning the total dissimilarity in species composition (represented by the Sorensen index) into its turnover and nestedness components using 100 samples of 10 sites from each geomorphic zone. The analysis was conducted on Sorensen dissimilarity matrix using a betapart package available in R CRAN (*Baselga et al., 2017*).

Statistical analysis

The statistical approach we use for the comparative analysis of benthic parameters and their geomorphological settings is similar to the method described by *Medina-Valmaseda et al. (2020)* who analyzed the geomorphic patterns of coral species at a single site, Punta Maroma. The main goal in using multivariate analysis in that study, and in this one, is to minimize method-bias of benthic surveys from multivariate-based analyses of ecological, abundance-based variables, which include a narrow set of pre-treatments and transforming of the raw data (*e.g.*, standardization). For the multivariate pre-treatment, we
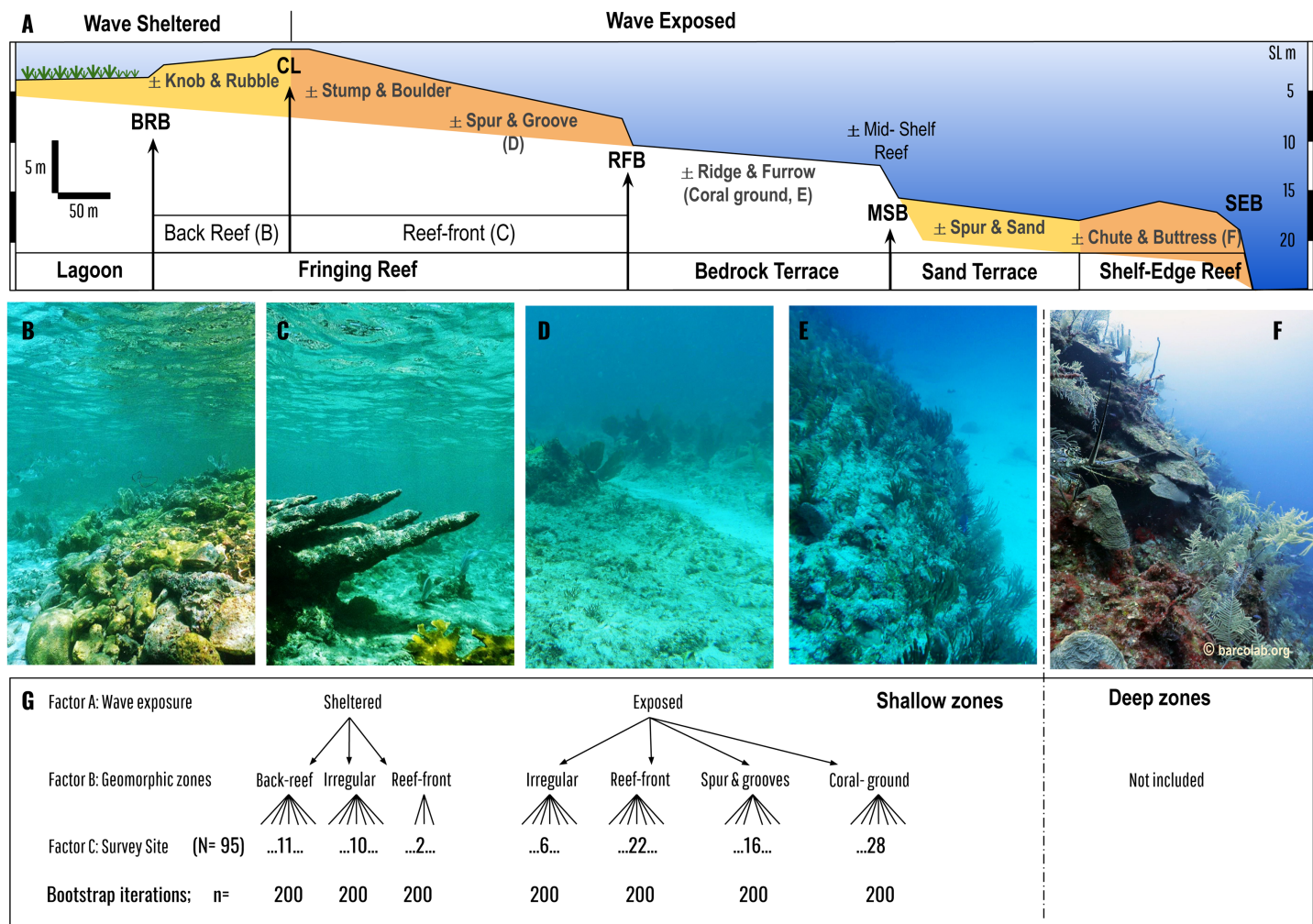
Figure 2 **Geomorphic zonation of an idealized shelf showing shallow reef and benthic zones typical of Mesoamerican reef seascapes (following** *Blanchon et al., 2017*). Zones are delineated by slope breaks: Back-Reef break (BRB), Crestline (CL), Reef-Front break (RFB), Mid-Shelf break (MSB), and Shelf-Edge 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 & Jones (1995)* for detailed 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). Photos (B–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). (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).

Full-size 🖼 DOI: 10.7717/peerj.12590/fig-2

choose a medium level (square-root) of data transformation. Further transformation is followed by an ordination process where we construct the correspondent Bray–Curtis matrix of similarities. All subsequent multivariate statistical analyses and graphical outputs are performed and constructed using Plymouth Routines in Multivariate Ecological Research (Primer-e version 7.0.13, serial number 4901, *Clarke & Gorley, 2015*).

To compare overall coral cover and related coral species contribution to relative cover of the communities between geomorphic zones, we conduct an 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, with three sheltered and four exposed. The experimental design consists of three factors (Fig. 2C): Factor A: wave exposure (fixed with a = 2 levels: sheltered and exposed), Factor B: Geomorphic zones (random, nested in wave exposure with five levels: irregular, coral-ground, spur & grooves, reef-front and back reef), 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 9,999 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 (*Anderson, Ellingsen & McArdle, 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 & Warwick, 1994*; *Clarke et al., 2014*). The results are presented through the metric MDS of bootstrapped averages for 95% region estimates. Bootstrap averages test iteratively resample each group by its geomorphic zone 200 times, creating a plot of 4 m 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 (Fig. 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, Vitense & Johnson, 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 & Gorley, 2006*). Finally, we normalize data to place each variable on the same dimensionless scale (for example, *Clarke, Tweedley & Valesini, 2014*). 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 & Anderson, 1999*). The DISTLM test includes the Bray–Curtis matrices of previously square transformed data of coral species distribution and logarithmic 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 & Anderson, 1999*; *McArdle & 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 and contain a total of 40 coral species. As shown in Fig. 3 results of β-diversity analysis show high levels of Total β-diversity (Fig. 3A, solid lines) for every geomorphic zone with high values and contribution of their turnover component (Fig. 3B, dashed lines) and low values for their nestedness-resultant component (Fig. 3B). Such results indicate that there is a low proportion of shared species between coral communities from adjacent geomorphic zones with a similar number of species. Although differences in taxonomic β-diversity values are clear between coral communities from sheltered back reef and exposed coral-ground zones, these are diffuse and overlapping for the communities from exposed reef front and spur & groove zones. The lower value of the nestedness-resultant fraction of Sorensen dissimilarity belongs to coral communities from sheltered back reef zones, whereas those from the irregular zones of wave-sheltered environments and wave-exposed spur & groove and coral-ground zones show almost identical patterns, indicating a confluence in these components for the exposed zones (Fig. 3B). Under the setting conditions of the β-diversity test, more sites were requested for sampling in the available datasets from two of the seven geomorphic zones. Results of the
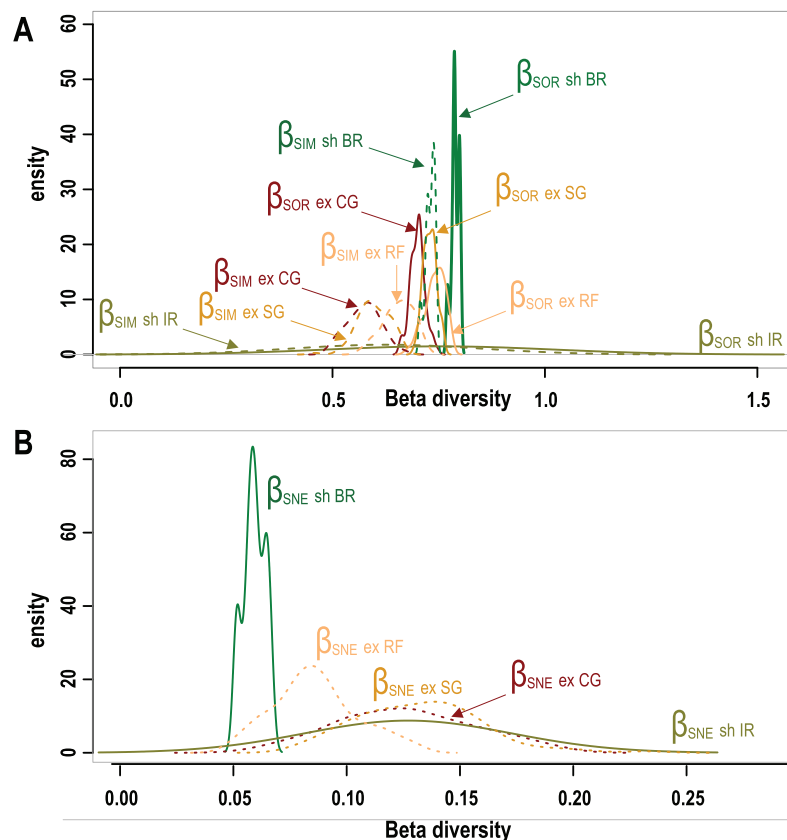
Figure 3 Taxonomic β-diversity of geomorphic zones and its components after _Baselga (2012)_.
(A) The overall β-diversity, measured as Sorensen dissimilarity β_{SOR} (solid lines) and values of the turnover component, measured as Simpson dissimilarity β_{SIM} (dashed lines). (B) Values of the nestedness-resultant fraction of the Sorensen dissimilarity β_{SNE}. Note singular patterns in wave-sheltered back reef zones, and the similar patterns of all wave exposed zones (dotted lines) with that of the wave-sheltered irregular zone. Geomorphic zones by wave-exposure follow the colour code in Fig. 1: the prefixes "sh" and "ex" correspond to wave-sheltered and wave-exposed zones respectively. Zones are denoted by BR - back reef, IR - irregular zone, RF - reef front, SG - spur & grooves, CG - coral ground.
Full-size 🖼 DOI: 10.7717/peerj.12590/fig-3

test are therefore unavailable for wave-exposed irregular zones (6 sampling sites), and wave-sheltered reef fronts (2 sampling sites).

The results of the PERMANOVA test indicates that there are no significant differences in overall coral cover between wave sheltered and wave-exposed geomorphic zones (P(perm) = 0.39; Fig. 4A; Data S1), although when species identity is included in the relative composition analysis, there are significant differences between geomorphic zones (Fig. 4B). The results of the asymmetrical PERMANOVA test including the three terms 'wave exposure', 'Geo zone (wave exposure)' and 'site (Geo zone (wave exposure))' show that there are marginal differences among the wave exposure environments in assemblage structure (P(perm) = 0.06; P(MC) = 0.07) whereas there is a significant variability among assemblage structure from the geomorphic zones (P(perm) and P(MC) < 0.01, Fig. 4A; Data S2). The estimates of components of variation (S) for the three orthogonal factors are wave exposure: 115.82; Geo zone nested in wave exposure: 214.98;
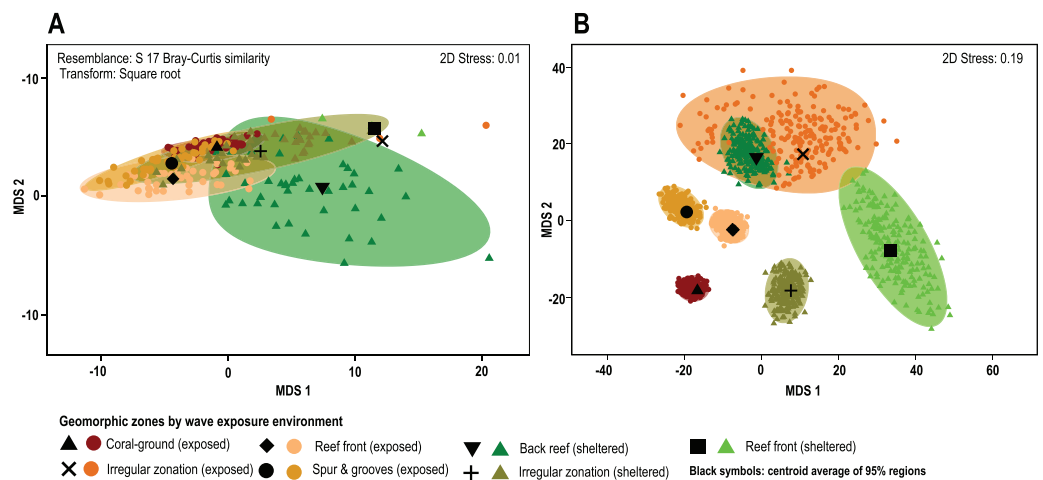
Figure 4 Coral cover patterns by geomorphic zone. (A) The similarity of overall coral cover for each zone type and wave exposure, using a metric MDS of 'whole sample' bootstrap averages resampling the n-transects of each sampling site 200 times (arranged by geomorphic zones and wave environment). nMDS shows the approximate 95% region estimates fitted to the bootstrap averages and the relative estimated position of centroids for each group (black symbols). (B) The 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 complete species homogenization across the reef seascape (3D stress: 0.08).   Full-size ☒ DOI: 10.7717/peerj.12590/fig-4

and site nested in Geo zone nested in wave exposure: 875.33. The site factor therefore contributes most to differences in species contribution, followed by the geomorphic zone, with wave exposure having the least control.

A posteriori pairwise PERMDISP test at the LCC level shows homogeneity of variance in all groups (F: 1.49, df1: 6, df2: 84; p(perm): 0.3422; Data S3), whereas the species contribution level shows heterogeneity in data variance involving pairwise tests for single or combined irregular and exposed zones (F: 13.23, df1: 6, df2: 543; p(perm): <0.01; Data S4). Other cases, including the irregular and combined sheltered/exposed geomorphic zones, show homogeneity in data variances (F: 13.23, df1: 6, df2: 543; p(perm): <0.01; Fig. 4B). In total 61% of possible pairwise tests show homogeneity in data variance and do not show a particular trend under the current PERMANOVA design. This indicates that there are differences in coral-species distribution between geomorphic zones (PERMANOVA), and in the variance of data distribution (PERMDISP) in several zones within the same environments (Fig. 4, Data S4).

The contribution of individual species to observed differences is assessed using the SIMPER test (Data S5). Results show that in exposed geomorphic zones three species overlap: *Agaricia agaricites, Porites astreoides* and *Siderastrea siderea* (Average similarity: 30.0) with relative contributions of 32.2%, 24.3% and 15.1% respectively. In sheltered zones another trio of species overlap, *P. astreoides, Orbicella annularis* and *Agaricia agaricites* (Average similarity 25.7) with relative contributions of 49.0%, 18.5% and 8.4% respectively (Data S1 to Data S5). Interestingly, an almost identical group of species accounts for the 81.2% average dissimilarity between samples. In terms of dissimilarity, only four species (*S. siderea, Porites astreoides, O. annularis* and *A. agaricites*), which
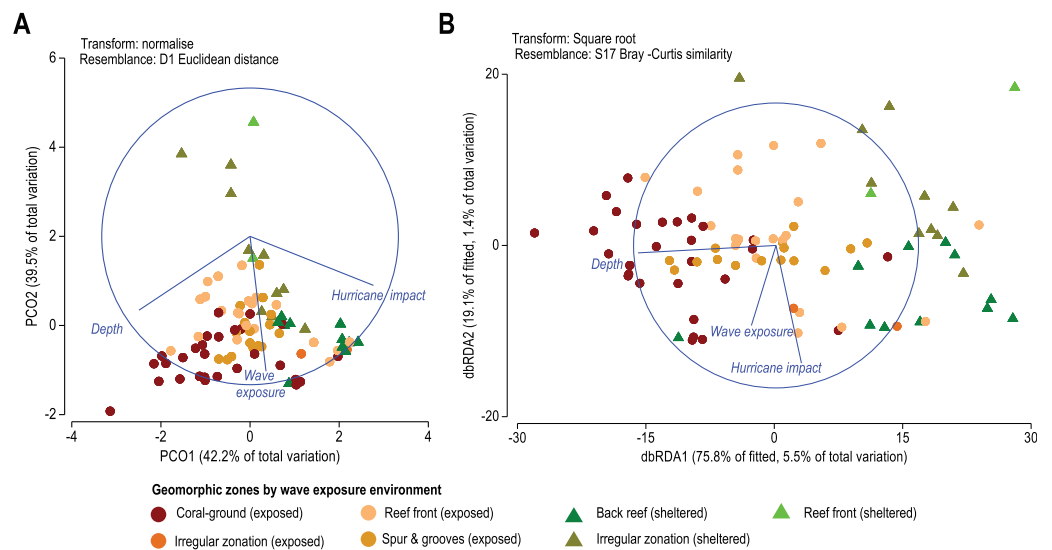
Figure 5 (A) Principal Coordinates Analysis (PCO) shows the multivariate environmental data cloud of three selected variables, depth, wave exposure and hurricane impact. Note the first two axes explain 81.6% of the internal variability of the three variables with depth contrasting with hurricane and depth and wave exposure acting differently. (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.

Full-size 🖼 DOI: 10.7717/peerj.12590/fig-5

contribute ~10%, form roughly 53% of the differences between samples. Overall, across all wave exposure zones, the largest average similarity of 34.9% corresponds to the exposed Coral-ground zone, and the lowest 18.2% to the sheltered Back-reef zone.

Coral species patterns and extrinsic factors

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

On a regional scale, all sites are exposed to a similar wave-exposure regime regardless of geomorphic zone, whereas hurricane impact varies between sites (Fig. 5). When analyzed by geomorphic zone and wave exposure, the average site depth varies from 1.8 ± 2.9 m in sheltered reef-front zones, to 11.2 ± 4.2 m in exposed coral-ground zones. Chronic stress derived from wave-exposure for these sites varies between 5.9 ± 0.9 and 7.4 ± 0.2 J m^{-3}. Whereas acute mechanical stress derived from hurricane frequency in the last 157 years (1851–2008) varies between 11 ± 2 years and 20 ± 2.8 years (Table 1). Regional patterns of three selected environmental data are presented in the Principal Coordinates Analysis (PCO) of Fig. 5. It shows that the first two axes explain 81.6% of the internal variability of these three environmental variables, indicating that the 2-d ordination is likely to have captured the majority of the patterns of multidimensional data variation. Accordingly, the depth of the reef site and hurricane impact explain 42.2% of

variations of the PCO1 axis, and wave energy exposure alone explains 39.5% of the PCO2 axis. In addition, depth and hurricane impact appear to act inversely over coral species patterns (Fig. 5A).

Results from the DISTLM marginal tests (Data S6) show how much can be explained by each abiotic variable alone, ignoring other variables. Tests show that the depth of reef sites exerts the highest influence explaining 5.5% of the overall variability in coral species contribution ($p < 0.01$, Data S4A, Fig. 5B). Wave exposure and the number of major hurricane impacts when each is considered alone explain roughly 1% to 1.5% ($p < 0.01$, Data S4A, Fig. 5B) of variability in species contribution to each geomorphic zone. These results indicate that spatial patterns in coral species contribution by geomorphic zones are still responsive to these three environmental variables.

DISCUSSION

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

When looking at similarities in the distribution of reef-building species, the Beta-diversity analysis provides a comprehensive overview of how it varies at the scales of tens to hundreds of meters encompassing the geomorphic framework of the MART. The comparison of compositional differences between geomorphic zones, further partitioned into turnover and nestedness after *Baselga et al. (2017)*, allows further understanding of how coral biodiversity is assembled across wave-energy gradients of sheltered and exposed geomorphic zones. These results are consistent with previous studies indicating that changes in species composition at small scales occurs as a consequence of historical spatial constraints or environmental sorting, for example, in response to depth (*e.g.*, *Izsak & Price, 2001*; *Ellingsen & Gray, 2002*). Similarly, other studies have also highlighted the relevance of environmental drivers in configuring local coral assemblages (*Murdoch & Aronson, 1999*; *Williams et al., 2015a*; *Miyazawa et al., 2020*). Our findings thus expand the comprehension of the factors underlying the turnover in species distribution in concordance with the geomorphic zonation.

We recognize that these factors generate a weak signal in the degraded coral community and this is likely impacted by the methodological protocol. For example, only a limited number of long-term variables were considered in analysing the species distribution patterns and, two of these (waves and hurricanes), exhibit significant variability over short

temporal scales. Nevertheless, both have been reported as major environmental drivers of ecological processes including species zonation (*Geister, 1977*; *Hughes et al., 2019*). Moreover, the impact of such disturbances creates an adaptive biotic response by influencing the life-history traits of coral assemblages and creating scale-dependent patterns of species distribution, with some being better adapted to hurricane impacts (*e.g.*, *Chollett & Mumby, 2012*). In addition, the result is also consistent with multiple reports of the increasingly important role that tropical cyclones play in shaping coral reef ecosystems at both short- and long-term scales (*Blanchon, Jones & Kalbfleisch, 1997*; *Lugo, Rogers & Nixon, 2000*; *Blanchon et al., 2017*; *Hogan et al., 2020*; *Puotinen et al., 2020*). Moreover, several schemes have proposed an adaptive response of coral assemblages to wave exposure regimes (*e.g.*, *Adey & Burke, 1977*; *Geister, 1977*). To some extent, our results augment these schemes by assigning a geomorphic framework and providing an alternative approach to imprecisely defined species-zonation limits. However, wave-fetch becomes saturated on a regional scale and its role in these schemes has been questioned (*Adey, 1978*). If this is accurate then it could help explain the linkage weakness in Mesoamerican reefs.

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

The impact of reef geomorphology on coral species composition has been largely ignored in both original (local) and regional analyses (*e.g.*, *Rioja-Nieto & 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., 2015b*; *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, confirming 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 showed 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 & 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). Nevertheless, 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.

ACKNOWLEDGEMENTS

ADDITIONAL INFORMATION AND DECLARATIONS

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Alexis Enrique Medina-Valmaseda conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored and reviewed drafts of the paper, and approved the final draft.
- Paul Blanchon conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored and reviewed drafts of the paper, and approved the final draft.
- Lorenzo Alvarez-Filip performed the experiments, reviewed drafts of the paper, and approved the final draft.
- Esmeralda Pérez-Cervantes performed the experiments, analyzed the data, prepared figures and/or tables, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:
The raw data is available at GitHub:
https://github.com/AlexisMedina2019/PeerJ-60115.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.12590#supplemental-information.

REFERENCES

Álvarez Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* **276(1669)**:3019–3025 DOI 10.1098/rspb.2009.0339.

Adey WH. 1978. Algal ridges of the Caribbean sea and West Indies. *Phycologia* **17(4)**:361–367 DOI 10.2216/i0031-8884-17-4-361.1.

Adey WH, Burke RB. 1977. Holocene bioherms of Lesser Antilles—geologic control of development. *AAPG Studies in Geology* **4**:6781.

Almada-Villela P, Sale P, Gold-Bouchot G, Kjerfve B. 2003. Manual of methods for the MBRS synoptic monitoring program. In: *Selected Methods for Monitoring Physical and Biological Parameters for Use in the Mesoamerican Region*, Belize: Mesoamerican Barrier Reef Systems Project, 155.

Alvarez-Filip L, Estrada-Saldivar N, Pérez-Cervantes E, Molina-Hernández A, González-Barrios FJ. 2019. A rapid spread of the stony coral tissue loss disease outbreak in the Mexican Caribbean. *PeerJ* **7(1)**:e8069 DOI 10.7717/peerj.8069.

Anderson MJ. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* **62(1)**:245–253 DOI 10.1111/j.1541-0420.2005.00440.x.

Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* **9(6)**:683–693 DOI 10.1111/j.1461-0248.2006.00926.x.

Aronson RB, Precht WF. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* **23(3)**:326–346 DOI 10.1017/S0094837300019710.

Aronson RB, Precht WF. 2001. White-band disease and the changing face of Caribbean coral reefs. In: *The Ecology and Etiology of Newly Emerging Marine Diseases*, Berlin: Springer, 25–38.

Baselga A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **21(12)**:1223–1232 DOI 10.1111/j.1466-8238.2011.00756.x.

Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F, Logez M, Henriques-Silva R. 2017. Partitioning beta diversity into turnover and nestedness components. Package betapart, Version 1–4.

Bayraktarov E, Stewart-Sinclair PJ, Brisbane S, Boström-Einarsson L, Saunders MI, Lovelock CE, Possingham HP, Mumby PJ, Wilson KA. 2019. Motivations, success, and cost of coral reef restoration. *Restoration Ecology* **27(5)**:981–991 DOI 10.1111/rec.12977.

Bellwood DR, Hughes TP, Folke C, Nyström M. 2004. Confronting the coral reef crisis. *Nature* **429(6994)**:827–833 DOI 10.1038/nature02691.

Blanchon P. 2011. Geomorphic zonation. In: Hopley D, ed. *Encyclopedia of Modern Coral Reefs*. Berlin: Springer, 469–486.

Blanchon P, Jones B. 1995. Marine-planation terraces on the shelf around Grand Cayman: a result of stepped holocene sea-level rise. *Journal of Coastal Research* **11(1)**:1–33 DOI 10.7939/R34T6FJ3N.

Blanchon P, Jones B, Kalbfleisch W. 1997. Anatomy of a fringing reef around Grand Cayman; storm rubble, not coral framework. *Journal of Sedimentary Research* **67(1)**:1–16 DOI 10.1306/d42684d7-2b26-11d7-8648000102c1865d.

Blanchon P, Richards S, Bernal JP, Cerdeira-Estrada S, Ibarra M, Corona-Martnez L, Martell-Dubois R. 2017. Retrograde accretion of a Caribbean fringing reef controlled by Hurricanes and sea-level rise. *Frontiers in Earth Science* **5**:78 DOI 10.3389/feart.2017.00078.

Bruckner A, Bruckner R. 2006. The recent decline of Montastraea annularis (complex) coral populations in Western Curaçao: a cause for concern? *Revista de Biologia Tropical* **54**:45–58 DOI 10.15517/rbt.v54i3.26870.

Bruckner AW. 2012. Static measurements of the resilience of Caribbean coral populations. *Revista de Biologia Tropical* **60**:39–57 DOI 10.15517/rbt.v60i0.19844.

Burke R. 1982. Reconnaissance study of the geomorphology and benthic communities of the outer barrier reef platform, Belize. In: Rützler K, Macintyre IG, eds. *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize*. Structures and communities. Vol. 1. Washington, D.C.: Smithsonian Institution Press, 509–526.

Chollett I, Mumby P. 2012. Predicting the distribution of Montastraea reefs using wave exposure. *Coral Reefs* **31(2)**:493–503 DOI 10.1007/s00338-011-0867-7.

Chollett I, Mumby PJ, Müller-Karger FE, Hu C. 2012. Physical environments of the Caribbean Sea. *Limnology and Oceanography* **57(4)**:1233–1244 DOI 10.4319/lo.2012.57.4.1233.

Clarke K, Gorley R. 2006. PRIMER v6: user manual/tutorial (Plymouth Routines in Multivariate Ecological Research). PRIMER-E, Plymouth.

Clarke K, Gorley R. 2015. Getting started with primer v7. PRIMER-E. Plymouth, Plymouth Marine Laboratory 20.

Clarke K, Warwick R. 1994. Similarity-based testing for community pattern: the two-way layout with no replication. *Marine Biology* **118(1)**:167–176 DOI 10.1007/BF00699231.

Clarke KR, Gorley R, Somerfield PJ, Warwick R. 2014. *Change in marine communities: an approach to statistical analysis and interpretation*. Auckland: Primer-E Ltd.

Clarke KR, Tweedley JR, Valesini FJ. 2014. Simple shade plots aid better long-term choices of data pre-treatment in multivariate assemblage studies. *Journal of the Marine Biological Association of the United Kingdom* **94(01)**:1–16 DOI 10.1017/S0025315413001227.

Contreras-Silva AI, Tilstra A, Migani V, Thiel A, Pérez-Cervantes E, Estrada-Saldvar N, Elias-Ilosvay X, Mott C, Alvarez-Filip L, Wild C. 2020. A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean. *Scientific Reports* **10(1)**:1–12 DOI 10.1038/s41598-020-65801-8.

Côté I, Gill J, Gardner T, Watkinson A. 2005. Measuring coral reef decline through meta-analyses. *Philosophical Transactions of the Royal Society B: Biological Sciences* **360(1454)**:385–395 DOI 10.1098/rstb.2004.1591.

Cramer KL, O'Dea A, Leonard-Pingel JS, Norris RD. 2020. Millennial-scale change in the structure of a Caribbean reef ecosystem and the role of human and natural disturbance. *Ecography* **43(2)**:283–293 DOI 10.1111/ecog.04722.

Dietzel A, Bode M, Connolly SR, Hughes TP. 2020. Long-term shifts in the colony size structure of coral populations along the great barrier reef. *Proceedings of the Royal Society B: Biological sciences* **287(1936)**:20201432 DOI 10.1098/rspb.2020.1432.

Edmunds PJ, Bruno JF. 1996. The importance of sampling scale in ecology: kilometer-wide variation in coral reef communities. *Marine Ecology Progress Series* **143**:165–171 DOI 10.3354/meps143165.

Edwards AJ. 2010. *Reef rehabilitation manual*. St. Lucia: Coral Reef Targeted Research & Capacity Building for Management Program.

Ellingsen K, Gray Js. 2002. Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? *Journal of Animal Ecology* **71(3)**:373–389 DOI 10.1046/j.1365-2656.2002.00606.x.

Ellis JI, Jamil T, Anlauf H, Coker DJ, Curdia J, Hewitt J, Jones BH, Krokos G, Kürten B, Hariprasad D, Roth F, Carvalho S, Hoteit I. 2019. Multiple stressor effects on coral reef ecosystems. *Global Change Biology* **25(12)**:4131–4146 DOI 10.1111/gcb.14819.

Estrada-Saldívar N, Jordán-Dalhgren E, Rodríguez-Martínez RE, Perry C, Álvarez Filip L. 2019. Functional consequences of the long-term decline of reef-building corals in the Caribbean: evidence of across-reef functional convergence. *Royal Society Open Science* **6(10)**:190298 DOI 10.1098/rsos.190298.

Fieberg J, Rieger RH, Zicus MC, Schildcrout JS. 2009. Regression modelling of correlated data in ecology: subject-specific and population averaged response patterns. *Journal of Applied Ecology* **46(5)**:1018–1025 DOI 10.1111/j.1365-2664.2009.01692.x.

Fieberg JR, Vitense K, Johnson DH. 2020. Resampling-based methods for biologists. *PeerJ* **8(2)**:e9089 DOI 10.7717/peerj.9089.

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301(5635)**:958–960 DOI 10.1126/science.1086050.

Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. In: *Proceedings of the 3rd International Coral Reef Symposium*, Vol. 1. 23–29.

Gladfelter WB. 1982. White-band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. *Bulletin of Marine Science* **32(2)**:639–643 DOI 10.1007/978-94-017-3284-0_2.

González-Barrios FJ, Cabral-Tena RA, Alvarez-Filip L. 2021. Recovery disparity between coral cover and the physical functionality of reefs with impaired coral assemblages. *Global Change Biology* **27(3)**:640–651 DOI 10.1111/gcb.15431.

Gower JC. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* **53(3–4)**:325–338 DOI 10.2307/2333639.

Grigg RW, Dollar SJ. 1990. Natural and anthropogenic disturbance on coral reefs. *Ecosystems of the World* **25**:439–452 DOI 10.1515/9780824844264-042.

Guzmán HM, Jackson JB, Weil E. 1991. Short-term ecological consequences of a major oil spill on Panamanian subtidal reef corals. *Coral Reefs* **10(1)**:1–12 DOI 10.1007/BF00301900.

Hein MY, Beeden R, Birtles A, Gardiner NM, Le Berre T, Levy J, Marshall N, Scott CM, Terry L, Willis BL. 2020. Coral restoration effectiveness: multiregional snapshots of the long-term responses of coral assemblages to restoration. *Diversity* **12(4)**:153 DOI 10.3390/d12040153.

Hogan JA, Feagin RA, Starr G, Ross M, Lin T-C, O'Connell C, Huff TP, Stauffer BA, Robinson KL, Lara MC, Xue J, Reese BK, Geist SJ, Whitman ER, Douglas S, Congdon VM, Reustle JW, Smith RS, Lagomasino D, Strickland BA, Wilson SS, Proffitt CE, Hogan JD, Branoff BL, Armitage AR, Rush SA, Santos RO, Campos-Cerqueira M, Montagna PA, Erisman B, Walker L, Silver WL, Crowl TA, Wetz M, Hall N, Zou X, Pennings SC, Wang L-J, Chang C-T, Leon M, Mcdowell WH, Kominoski JS, Patrick CJ. 2020. A research framework to integrate cross-ecosystem responses to tropical cyclones. *BioScience* **70(6)**:477–489 DOI 10.1093/biosci/biaa034.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265(5178)**:1547–1551 DOI 10.1126/science.265.5178.1547.

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JB, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR,

Pandolfi JM, Rosen B, Roughgarden J. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301(5635)**:929–933 DOI 10.1126/science.1085046.

Hughes TP, Graham NA, Jackson JB, Mumby PJ, Steneck RS. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution* **25(11)**:633–642 DOI 10.1016/j.tree.2010.07.011.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A, Hill T, Hoey AS, Hoogenboom MO, Jacobson M, Kerswell A, Madin JS, Mieog A, Paley AS, Pratchett MS, Torda G, Woods RM. 2019. Global warming impairs stock-recruitment dynamics of corals. *Nature* **568(7752)**:387–390 DOI 10.1038/s41586-019-1081-y.

Izsak C, Price A. 2001. Measuring b-diversity using a taxonomic similarity index, and its relation to spatial scale. *Marine Ecology Progress Series* **215**:69–77 DOI 10.3354/meps215069.

Jackson J, Donovan M, Cramer K, Lam L. 2014. *Status and trends of Caribbean coral reefs-1970–2012–2014 Caribbean coral reefs-status report 1970–2012 (1)*. Gland: Global Coral Reef Monitoring Network, IUCN.

James NP, Ginsburg RN. 1979. *The seaward margin of Belize barrier and Atoll reefs: morphology, sedimentology, organism distribution, and late quaternary history*. Hoboken: Blackwell Scientific.

Karlson R, Hurd L. 1993. Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs* **12(3–4)**:117–125 DOI 10.1007/BF00334469.

Knowlton N, Lang JC, Rooney MC, Clifford P. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. *Nature* **294(5838)**:251–252 DOI 10.1038/294251a0.

Kuffner IB, Toth LT. 2016. A geological perspective on the degradation and conservation of Western Atlantic coral reefs. *Conservation Biology* **30(4)**:706–715 DOI 10.1111/cobi.12725.

Kuffner IB, Toth LT, Hudson JH, Goodwin WB, Stathakopoulos A, Bartlett LA, Whitcher EM. 2019. Improving estimates of coral reef construction and erosion with in situ measurements. *Limnology and Oceanography* **64(5)**:2283–2294 DOI 10.1002/lno.11184.

Lang JC, Marks KW, Kramer PR, Kramer PA, Ginsburg RN. 2012. *Protocolos AGRRA version 5.5*. Big Pine Key: Ocean Research & Education.

Legendre P, Anderson MJ. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69(1)**:1–24 DOI 10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2.

Lessios H, Cubit J, Robertson D, Shulman M, Parker M, Garrity S, Levings S. 1984. Mass mortality of diadema antillarum on the Caribbean coast of panama. *Coral Reefs* **3(4)**:173–182 DOI 10.1007/BF00288252.

Lewis JB. 1984. The Acropora inheritance: a reinterpretation of the development of fringing reefs in Barbados, West Indies. *Coral Reefs* **3(3)**:117–122 DOI 10.1007/BF00301955.

Lugo AE, Rogers CS, Nixon SW. 2000. Hurricanes, coral reefs and rainforests: resistance, ruin and recovery in the Caribbean. *AMBIO: A Journal of the Human Environment* **29(2)**:106–114 DOI 10.1579/0044-7447-29.2.106.

Macintyre I, Glynn P. 1976. Evolution of modern Caribbean fringing reef, Galeta Point, Panama. *AAPG Bulletin* **60(7)**:1054–1072 DOI 10.1306/c1ea3618-16c9-11d7-8645000102c1865d.

McArdle BH, Anderson MJ. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82(1)**:290–297 DOI 10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

McWilliam M, Hoogenboom MO, Baird AH, Kuo C-Y, Madin JS, Hughes TP. 2018. Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of The National Academy of Sciences* **115(12)**:3084–3089 DOI 10.1073/pnas.1716643115.

Medina-Valmaseda AE, Rodríguez-Martínez RE, Alvarez-Filip L, Jordan-Dahlgren E, Blanchon P. 2020. The role of geomorphic zonation in long-term changes in coral-community structure on a Caribbean fringing reef. *PeerJ* **8(1)**:e10103 DOI 10.7717/peerj.10103.

Miyazawa E, Montilla LM, Agudo-Adriani EA, Ascanio A, Mariño-Briceño G, Croquer A. 2020. On the importance of spatial scales on beta diversity of coral assemblages: a study from Venezuelan coral reefs. *PeerJ* **8(2)**:e9082 DOI 10.7717/peerj.9082.

Muller EM, Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, Álvarez-Filip L, Baca BJ, Bartles E, Bastidas C. 2010. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLOS ONE* **5(11)**:e13969 DOI 10.1371/journal.pone.0013969.

Murdoch TJ, Aronson RB. 1999. Scale-dependent spatial variability of coral assemblages along the Florida reef tract. *Coral Reefs* **18(4)**:341–351 DOI 10.1007/s003380050210.

Perry CT. 1999. Reef framework preservation in four contrasting modern reef environments, Discovery Bay. *Jamaica Journal of Coastal Research* **15(3)**:796–812 DOI 10.1038/ncomms2409.

Perry CT, Alvarez-Filip L. 2019. Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology* **33(6)**:976–988 DOI 10.1111/1365-2435.13247.

Puotinen M, Drost E, Lowe R, Depczynski M, Radford B, Heyward A, Gilmour J. 2020. Towards modelling the future risk of cyclone wave damage to the world's coral reefs. *Global Change Biology* **26(8)**:4302–4315 DOI 10.1111/gcb.15136.

QGIS Development Team. 2020. *QGIS geographic information system*. Beaverton: Open Source Geospatial Foundation.

Rioja-Nieto R, Álvarez-Filip L. 2019. Coral reef systems of the Mexican Caribbean: status, recent trends and conservation. *Marine Pollution Bulletin* **140**:616–625 DOI 10.1016/j.marpolbul.2018.07.005.

Rodríguez-Martínez RE, Jordan-Garza AG, Maldonado MA, Blanchon P. 2011. Controls on coral-ground development along the Northern Mesoamerican Reef Tract. *PLOS ONE* **6(12)**:e28461 DOI 10.1371/journal.pone.0028461.

Rogers CS, Beets J. 2001. Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the us virgin islands. *Environmental Conservation* **28(4)**:312–322 DOI 10.1017/S0376892901000340.

Schutte VG, Selig ER, Bruno JF. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series* **402**:115–122 DOI 10.3354/meps08438.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, Mcmanus E, Molnar J, Recchia CA, Robertson J. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* **57(7)**:573–583 DOI 10.1641/B570707.

Spurgeon JP. 2001. Improving the economic effectiveness of coral reef restoration. *Bulletin of Marine Science* **69(2)**:1031–1045.

Tomascik T, Sander F. 1987. Effects of eutrophication on reef-building corals. *Marine Biology* **94(1)**:53–75 DOI 10.1007/BF00392900.

Torgerson WS. 1958. *Theory and methods of scaling*. New York: Wiley.

Toth LT, Stathakopoulos A, Kuffner IB, Ruzicka RR, Colella MA, Shinn EA. 2019. The unprecedented loss of Florida's reef-building corals and the emergence of a novel coral-reef assemblage. *Ecology* **100(9)**:e02781 DOI 10.1002/bes2.1615.

Viehman S, Thur SM, Piniak GA. 2009. Coral reef metrics and habitat equivalency analysis. *Ocean & Coastal Management* **52(3–4)**:181–188 DOI 10.1016/j.ocecoaman.2008.12.004.

Weil E. 2004. Coral reef diseases in the wider Caribbean. In: *Coral Health and Disease*, Berlin: Springer, 35–68.

Wiens JA. 1989. Spatial scaling in ecology. *Functional Ecology* **3(4)**:385–397 DOI 10.2307/2389612.

Williams SM, Chollett I, Roff G, Cortés J, Dryden CS, Mumby PJ. 2015a. Hierarchical spatial patterns in Caribbean reef benthic assemblages. *Journal of Biogeography* **42(7)**:1327–1335 DOI 10.1111/jbi.12509.

Williams SM, Mumby PJ, Chollett I, Cortés J. 2015b. Importance of differentiating Orbicella reefs from gorgonian plains for ecological assessments of Caribbean reefs. *Marine Ecology Progress Series* **530**:93–101 DOI 10.3354/meps11333.

Wood R. 2007. The changing fate of coral reefs: lessons from the deep past. In: *Geological Approaches to Coral Reef Ecology*, Berlin: Springer, 3–27.

Woodley JD, Chornesky E, Clifford P, Jackson J, Kaufman L, Knowlton N, Lang J, Pearson M, Porter J, Rooney M, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* **214(4522)**:749–755 DOI 10.1126/science.214.4522.749.