Reef condition and protection of coral diversity and evolutionary history in the marine protected areas of Southeastern Dominican Republic

Camilo Cortés-Useche [a,b,*], Aarón Israel Muñiz-Castillo [a], Johanna Calle-Triviño [a,b], Roshni Yathiraj [c], Jesús Ernesto Arias-González [a]

[a] *Centro de Investigación y de Estudios Avanzados del I.P.N., Unidad Mérida B.P. 73 CORDEMEX, C.P. 97310, Mérida, Yucatán, Mexico*
[b] *Fundación Dominicana de Estudios Marinos FUNDEMAR, Bayahibe, Dominican Republic*
[c] *ReefWatch Marine Conservation, Bandra West, Mumbai 400050, India*

ARTICLE INFO

ABSTRACT

Changes in structure and function of coral reefs are increasingly significant and few sites in the Caribbean can tolerate local and global stress factors. Therefore, we assessed coral reef condition indicators in reefs within and outside of MPAs in the southeastern Dominican Republic, considering benthic cover as well as the composition, diversity, recruitment, mortality, bleaching, the conservation status and evolutionary distinctiveness of coral species. In general, we found that reef condition indicators (coral and benthic cover, recruitment, bleaching, and mortality) within the MPAs showed better conditions than in the unprotected area (Boca Chica). Although the comparison between the Boca Chica area and the MPAs may present some spatial imbalance, these zones were chosen for the purpose of making a comparison with a previous baseline presented. In actuality these indicators found in the MPAs have improved when compared to results from previous reports (2001) in the same reefs and others in the Caribbean. Additionally, we found no evidence of massive bleaching during the El Niño-Southern Oscillation (ENSO) of 2015. Reef-building species belonging to *Orbicella* species complex dominate MPAs, while small colonies of *Pseudodiploria strigosa* and *Siderastrea siderea* with low structural complexity dominate the unprotected sites. Key findings include the potential offered by MPAs as a network; our results show that a combination of MPAs protect the variation in diversity and promote the conservation of coral while maintaining historical evolution traits. This study offers an evaluation framework that considers multiple aspects of relevance in the conservation of Caribbean coral reefs, presenting a baseline of ecological indicators in the southeastern region of the Dominican Republic. It also recognizes some protected reefs in this region that can be designated as places of hope, with excellent conditions in the coral community.

1. Introduction

Coral reefs are one of the most complex ecosystems in nature, with high productivity and biodiversity (Reaka-Kulda, 1997; Veron, 2000). Their social, economic and ecological values (Moberg and Folke, 1999) are essential to populations living along coastal regions (Wilkinson, 2008; Burke et al., 2011). Urban, industrial and agricultural development around coastal waters and even inland areas cause pollution and are particularly relevant for hard corals (Burke and Maidens, 2004; Heery et al., 2018), besides overfishing in the coastal zones cause habitat deterioration that negatively impact coral reefs (Hughes et al., 2003; Anthony et al., 2015). An increase in frequency and intensity of natural phenomena (e.g. hurricanes, storms) and/or global climate change (e.g. changes in temperature, pH and O_2) (Hoegh-Guldberg et al., 2007; Hughes et al., 2017) also negatively influence reefs. The reefs in the Caribbean are severely degraded and show clear signs of coral mortality and disease (Mora, 2008), including loss of coral cover (Carpenter et al., 2008) by more than 80% since the 1970s (Gardner et al., 2003; Jackson et al., 2014) and biodiversity (Pandolfi et al., 2003). In addition, the abundance of reef-building species such as *Acropora* and *Orbicella* species complex have drastically reduced (Porto-Hannes et al., 2015). *Acropora* species are catalogued by the International Union for Conservation of Nature (IUCN) as Critically Endangered Species and *Orbicella* species complex as Endangered Species (Aronson et al., 2008) and are included in Appendix II of the Convention

on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Calle-Triviño et al., 2018).

Given this situation, conservation efforts based on marine protected areas (MPAs) have been implemented (Mora et al., 2006). Most MPAs are management tools that restrict activities that extract resources and protect habitats from destructive practises (Watson et al., 2014). They improve coral cover, restore fishing productivity, increase reef resilience and sustain ecological processes at the local level (McCook et al., 2010; Claudet, 2011). They additionally aid in the recovery of ecosystem services (Selig and Bruno, 2010; Babcock et al., 2010; Mumby and Harborne, 2010; Mellin et al., 2016). However, even with the establishment of marine protected areas (MPAs), it is still unclear if they result in the facilitation of coral population recovery at a large scale (Cox et al., 2017). Though other studies show that MPAs do not provide ecological benefits or improvements in reefs (Graham et al., 2008; Selig and Bruno, 2010) and while evidence of the success of MPAs with indicators based on scleractinian corals and benthic functional groups is limited (Graham et al., 2006; McClanahan et al., 2006, 2012), in the context of global climate change (Anthony et al., 2015), the establishment of sites that protect ecosystems are still being challenged (Cinner et al., 2016). Analyses that assess the role of MPAs based on indicators of reef condition (i.e. coral and benthic cover, recruitment, bleaching, mortality) are crucial (McClanahan et al., 2012), as is the relevance of recognizing conservation priorities based on phylogenetic characteristics, diversity, and functionality of scleractinian coral species (Mellin et al., 2016; Mora et al., 2016; Mouillot et al., 2016). Implementing effective MPAs and MPA networks requires identifying the most relevant zones according to information on conservation purpose, capacity, and different biophysical and socioeconomic components that contribute to their success (Agardy et al., 2011; Cinner et al., 2016).

The coral reefs of the Dominican Republic form an ecosystem of high local and regional relevance; despite the existence of diverse protected areas that intend to ensure the prosperity of the reefs in this region (SINAP, 2014), recent studies are limited to the northern zone of the country (Eastwood et al., 2017) and the last evaluation for the south eastern (SE) MPAs was conducted 20 years ago between 1994 and 1997 (Chiappone, 2001). With this in mind, the aim of this study was to identify the condition of coral reefs based on health indicators and conservation priorities (i.e. diversity, conservation status and evolution distinctiveness of coral species) in an area with different levels of protection and high tourism development and fishing activities. This work evaluates these indicators for the first time in some coral reefs of the southeastern Dominican Republic, a region that has five different types of MPAs (868 900 ha): (1) Cotubanama Natural Park, (2) Guaraguao Catuano Natural Recreation Area, (3) Catalina Island Natural Monument, (4) Punta Bayahibe Natural Monument and (5) Southeastern Reefs Marine Sanctuary (SINAP, 2014). Our main intention was to identify if Dominican Republic's SE MPAs not only foster good reef condition through high live coral cover and low macroalgae cover but also protect the evolutionary history and the conservation of coral species diversity in the region.

2. Materials and methods

2.1. Study area and sites

Dominican Republic's SE reefs are dominated by coral patches near the coast (<2 km) (Chiappone, 2001). To examine the influence of protection, we studied 13 sites that have not been evaluated nor reported in scientific literature until now, seven test sites within MPAs and six unprotected sites in Boca Chica bay. The Boca Chica region was chosen because this region had already been characterized by Chiappone (2001), which allowed us to have a comparison with a previous baseline, adding that is the closest non-protected region with similar physical characteristics to the selected MPAs (Fig. 1).

MPAs in the area were established according to biophysical and socio-economic factors, more than 7 years ago and they have different management performance. To study the effects on independent MPAs, seven sites were selected randomly (Cayo Ratón, Punta Cacón, El Peñón, La Pared, Coralina, Atlantic Princess and Dominicus Reef), distributed in the five categories implemented by the Ministry of Environment and Natural Resources: (1) Cotubanamá Natural Park, (2) Guaraguao Catuano Recreation Natural Area, (3) Catalina Island Natural Monument, (4) Punta Bayahibe Natural Monument and (5) Southeastern Reefs Marine Sanctuary (Table 1). Fishing and boat transit are forbidden at Cayo Ratón since 2009 (Decree 499-09) in CNP. Organized tourism operators (12 dive centres) carry out diving activities and "artisanal" fishing at Punta Cacón, El Peñón, Atlantic Princess and Dominicus Reef sites. La Pared reef is at Catalina Island Natural Monument and suffers high levels of human pressure caused by tourism activities (tours and diving). In addition to urban waste; sediment and nutrients are flushed into this site from La Romana city. La Coralina site (PBNM) is located near Bayahibe municipality, an area with a high flow of boats, snorkeling activities, water sports, and "artisanal" fishing, an activity that involves 15 boats, 35 fishermen and approximately two landing points (Cortés-Useche et al., 2017). The six unprotected sites are in Boca Chica (BC), where all activities are allowed and unregulated. Within the Boca Chica bay there are 53 hotels with more than 2000 rooms, the region has no agricultural development and people completely rely on tourism and get food from fishing. Residents (approximate population 142 019) in Boca Chica are exposed to more severe poverty in terms of the life quality than others municipalities like La Romana or Bayahibe.

2.2. Sampling and data collection

Visual censuses were carried out through SCUBA diving at permanent stations from August 2015 to September 2016 at <12 m depth reefs (frontal reefs). For coral bleaching, surveys were performed in summer season (September to November) of 2015 during the high heat stress phase. The type of substrate was determined and the following attributes of the scleractinian coral communities were estimated: species richness, live coral cover, coral recruitment, bleaching (%), and mortality. The composition of the benthic community was determined using the point intercept transect method, deploying six 10 m transect lines, each 5 m apart; with intersection points placed every 0.25 m (Kramer, 2003; Lang et al., 2010, www.agrra.org) Coral recruitment (<2 cm colony diameter) was estimated using the PVC quadrant technique (25 × 25 cm quadrants). The quadrants were placed at five points along a transect line and each coral recruit was identified and measured. The number of colonies were sorted by species affected by coral diseases, evidence of bleaching or some type of mortality that was recorded for each transect (Lang et al., 2010). Benthic community average cover was categorized according to the Atlantic and Gulf Rapid Reef Assessment (AGRRA): live coral cover (LCC), macroalgae (MA), abiotic substrate (ASUB), crustose coralline algae (CCA), cyanobacteria (CYAN) and other invertebrates (OINV).

2.3. Data analysis

2.3.1. Benthos and coral species composition

Wisconsin double standardization was performed on coral cover assemblage data by species and benthos cover data, as
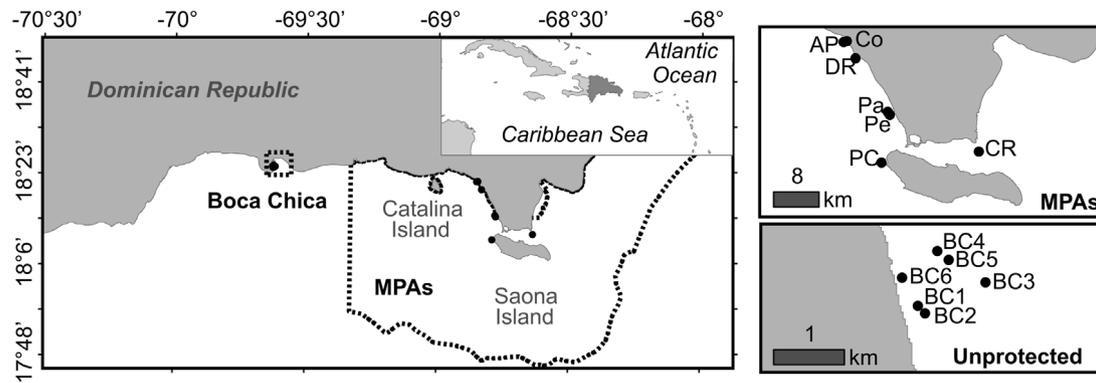
Fig. 1. Dominican Republic's SE Reefs. The seven protected sites (MPAs) are within the polygon covering an approximate area of 7855 km^2: Cayo Ratón (CR), Punta Cacón (PC), El Peñón (Pe), La Pared (Pa), Coralina (Co), Atlantic Princess (AP) and Dominicus Reef (DR). The six unprotected sites are in Boca Chica: (BC1, BC2, BC3, BC4, BC5, and BC6).

Table 1
List of codes and characteristics of the 13 study sites. CNP = Cotubanama Natural Park, GCNRA = Guaraguao Catuano Natural Recreation Area, CINM = Catalina Island Natural Monument, PBNM = Punta Bayahibe Natural Monument, SERMS = Southeastern Reefs Marine Sanctuary and NP = unprotected.

Category	IUCN	Site	Code	Year of legal establishment	Budget capacity	Staff capacity	Fishing	Dive intensity
CNP	II	Cayo Ratón	CR	1975	Below optimal	Inadequate	No-take zone	Closed
		Punta Cacón	PC	1975			Regulated	9/day
GCNRA	VI	El Peñón	Pe	1975	None	None	Regulated	34/day
CINM	III	La Pared	Pa	1995	Inadequate	Inadequate	Regulated	9/day
PBNM	III	Coralina	Co	2009	None	None	Regulated	Closed
SERMS	I	Atlantic Princess	AP	2009	None	None	Regulated	12/day
		Dominicus Reef	DR	2009			Regulated	61/day
NP	None	Boca Chica 1	BC1	No	None	None	All	Unknown
		Boca Chica 2	BC2	No			All	Unknown
		Boca Chica 3	BC3	No			All	Unknown
		Boca Chica 4	BC4	No			All	Unknown
		Boca Chica 5	BC5	No			All	Unknown
		Boca Chica 6	BC6	No			All	Unknown

has been recommended for subsequent analysis using multidimensional methods (Legendre and Gallagher, 2001; Legendre and Legendre, 2012). In the case of the coral species composition we eliminated the species *Orbicella annularis* because it was present only in Coralina (Co) with a relative high percentage of cover; which led to a distortion in the multidimensional representation due to the high dissimilarity that this species offered to the Coralina transects (Legendre and Legendre, 2012). The species *Orbicella annularis* was eliminated only for the multidimensional analysis, and subsequent diversity analyses this species was considered. Transformed and filtered data were used to estimate the Bray–Curtis dissimilarity coefficient (Legendre and Gallagher, 2001; Legendre and Legendre, 2012). Non-metric multidimensional scaling (NMDS) was used to graphically represent the order of sites for benthos and coral species coverage. The analysis was based on the 'meta-MDS' function and considered stability by minimizing stress; the main components were rotated to achieve a better representation of ordination (Legendre and Legendre, 2012).

To find out if differences between the types of coverage and coral species were present among sites, a permutational multivariate analysis of variance (PERMANOVA) was carried out. This analysis was based on 'adonis' function, following Anderson's equation (2001). Subsequently, a similarity percentage analysis (SIMPER) was carried out to find out which benthos functional groups and species contributed most to the differentiation between the levels of PERMANOVA-based factors. The analysis was based on the 'simper' function (Clarke, 1993; Warton et al., 2012). Both analyses were applied to the dissimilarity matrices based on transformed and filtered data and applying 999 permutations with $\alpha = 0.05$ value. All analysis mentioned above were based

on available functions in the 'vegan' library (Oksanen et al., 2016) statistics R program, version 3.3.1 (R Core Team, 2016).

2.3.2. Bleaching, mortality, and recruitment
To identify differences in coral bleaching, mortality and recruitment between MPAs and unprotected sites, a contrast hypothesis analysis was performed; the factor was protection category and the appointed value $\alpha = 0.05$. Coral bleaching and old mortality variables were represented by cover percentages and had no normality or homogeneity of variance within each category. For this reason, we decided to perform a square root transformation, allowing data normality and homogeneity for subsequent analysis by using a one-way ANOVA (Zar, 1999; Chambers et al., 1992). Recruitment and new mortality showed no apparent distribution and data transformation was not an option, so we applied a non-parametric analysis based on Wilcoxon rank sum test for independent samples (Hollander et al., 2015).

2.3.3. Diversity and evolutionarily distinct and globally endangered (EDGE) species indexes
In order to recognize the ecological relevance through indicators based on the richness and composition of coral species in each site, we evaluated three main aspects — alpha and beta diversity, and their Evolutionary Distinctiveness and Globally Endangered (EDGE) cumulative proportion of cover by site.

Alpha diversity was estimated based on the average coverage data of species in each site, using the untransformed and unfiltered database, indices were calculated with 0.0, 1.0 and 2.0 diversity orders with range equivalents to the Hill's numbers of richness, Shannon and Simpson diversity respectively (Hill, 1973;
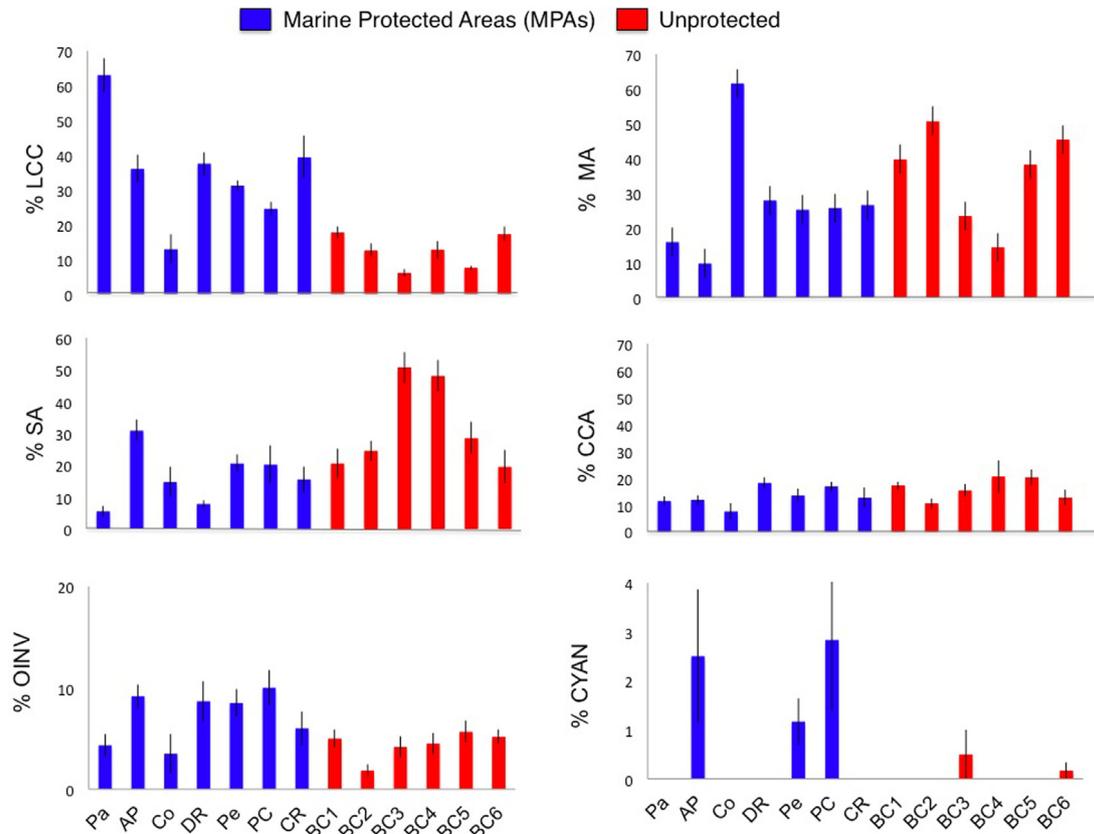
Fig. 2. Benthic cover (cover %) (mean ± SE): (a) live coral (LCC), (b) macroalgae (MA), (c) abiotic substrates (ASUB), (d) crustose coralline algae (CCA), (e) other invertebrates (OINV), (f) cyanobacteria (CYAN).

Jost, 2007). This index was expressed in units that are easier to interpret and of great ecological meaning (Hill, 1973; Jost, 2007). Analyses were based on 'entropart' library's 'divprofile' function (Marcon and Hérault, 2015).

An analysis of the local contribution to beta diversity (LCBD) was carried out with the purpose of establishing the percentage of contribution in each of the sites and identifying the uniqueness based on existing diversity (Legendre and De Cáceres, 2013). The study analysed the variation in Bray–Curtis dissimilarity matrix that was built for the composition of transformed coral data. However, in this case *Orbicella annularis* was considered in order to identify its importance in identifying how unique the sites were; this LCBD analysis gave a value of how unique the site was considering its contribution to variation in diversity, LCBD values indicate the sites that contribute more (or less) than the mean total beta diversity. The analysis was based on the 'adespatial' library (Dray et al., 2016).

To find out the degree of evolutionary history and the importance for conservation, we used the EDGE value proposed by Isaac et al. (2007). The starting point was a score given according to evolutionary distinctiveness (ED) weighted by the category established by the red list (GE), obtaining a value for the species of interest based on the following equation:

$$EDGE = In (1 + ED) + GE * In (2)$$

where the values represent threatened categories (GE) of the red list, with Least Concern = 0, Near Threatened and Conservation Dependent = 1, Vulnerable = 2, Endangered = 3, Critically Endangered = 4 (IUNC, 2017). EDGE values for coral species recorded in this work were obtained from the EDGE webpage (2018); they are explained and analysed in depth in the works of Huang (2012) and Curnick et al. (2015).

The priority for conservation EDGE index was calculated based on the EDGE value per species and the percentage of mean cover that each of the species represents at the site level, using the untransformed and unfiltered database. The index is represented by the following equation:

$$EDGE_{site} = \frac{\sum((CV\ spi/100) + EDGE\ spi)}{MAX\ EDGE\ value\ of\ the\ species}$$

EDGE$_{site}$ index is the summation of the product of the cover of species (CV) by its EDGE value divided by the maximum EDGE value for the species present. The maximum EDGE value is a constant represented by a score of 4.836 − the score for *Stephanocoenia intersepta* which has the maximum EDGE value of the species found in the studied MPAs. The product of this index is a ratio that goes from 0 to 1 and expresses the percentage of protection of evolutionary history and of conservation priority at site level.

All the analyses were carried out and plotted using the statistical program R version 3.3.1 (R Core Team, 2016).

3. Results

3.1. Benthic cover

Live coral cover (mean ± SE) (34.9 ± 5.8%) was greater in MPAs, especially in La Pared (63 ± 4.7%) and Cayo Ratón (39 ± 6.1%) sites; the lowest values were found in the unprotected areas studied (12.3 ± 1.9%) (Fig. 2a). Macroalgae showed higher coverage (35.3 ± 5.6%) within unprotected sites (BC1, BC2, BC3 y BC4) and at Coralina Reef (61 ± 5.4%), while the lowest values were found within MPAs (27.5 ± 6.2%) (Fig. 2b). Abiotic substrate cover (e.g. sand, rock, and rubble) had high values in the unprotected sites (31.9 ± 5.7%) and low values in MPAs (16.4 ± 3.2%)
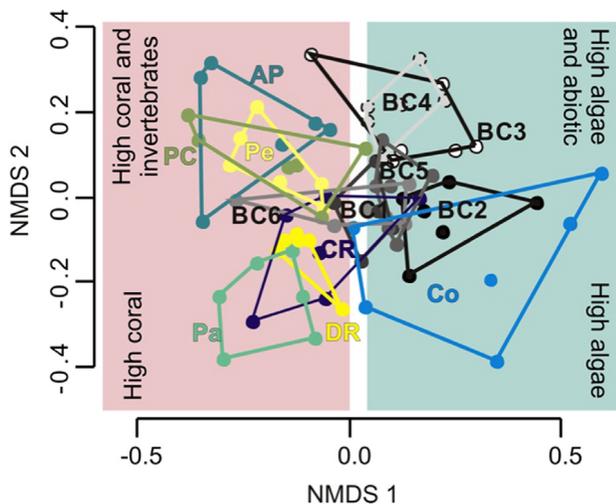
Fig. 3. (a) Non-metric multidimensional scaling (NMDS) of benthic cover. Table 1 shows site codes and protection category.

(Fig. 2c). Crustose coralline algae covered 16.1 ± 1.6% of the unprotected sites and 12.7 ± 1.5% within MPAs (Fig. 2d). Other invertebrates (e.g. sponges and soft corals) covered 4.4 ± 0.6% of the BC area and 7.5 ± 1.2% within MPAs (Fig. 2e). Cyanobacteria had low cover values 0.1 ± 0.1% in the BC area and 0.9 ± 0.5% within MPAs (Fig. 2f).

The MPA's cover composition was different from the benthic functional groups found in the unprotected sites, showing a greater cover of coral and coral with other invertebrates (with the exception of Coralina) than in unprotected sites where the macroalgae and abiotic substrate dominated the benthic cover (Fig. 3). We also found a significant difference between sites (PERMANOVA, Pseudo $F_{(12,65)}$ = 12.59, R^2 = 0.70 and permutated P = 0.01), where some sites like La Pared (Pa) and Cayo Ratón present considerably higher coral cover (SIMPER, permutated P < 0.05) We found that the coral cover, macroalgae and abiotic substrate was the most relevant benthic groups in the differentiation between sites.

3.2. Bleaching, mortality, and coral recruitment

In general, all the MPAs presented better coral health condition indicators based on bleaching and mortality. Besides, all MPAs presented high values of coral recruitment in contrast with unprotected sites. All study sites showed a low relative proportion of bleaching <12% (Fig. 4a). Differences in coral bleaching were observed between MPAs and unprotected sites (F $_{(1,11)}$ = 23.98, P = 0.0004), showing an average 1.2 ± 0.7% (SE) for MPAs while the average at the BC area was 7.6 ± 1.2% (Fig. 4b). New mortality (NM) was similar in MPAs (0.5 ± 0.4%, with values ranging from 0 to 3.2%) and in BC area (0.5 ± 0.3%, with values ranging from 0 to 2%) (Fig. 4c), and we found no differences in coral condition (Fig. 4d). Old mortality (OM) in MPAs was 1.4 ± 0.5% and had a range between 0 and 3.4%, but it was considerably greater in the BC area (F $_{(1,11)}$ = 11.7, P = 0.0057) with an average of 5.5 ± 1.3% with a range from 2 to 12% (Fig. 4e) (Fig. 4f). The density of coral recruits was low in all sites; MPAs had a mean 4 ± 1.4 ind/m^2, while the BC area showed a mean 2 ± 0.8 ind/m^2 (Fig. 4g). MPAs presented greater recruitment variation, with high values as compared to the BC area (W $_{(1,11)}$ = 14.5, P = 0.3874) (Fig. 4h). *Porites astreoides* and *A. agaricites* provided greater recruit abundance when compared with other species.

## 3.3. Diversity, EDGE index and composition of coral species

A total of 24 species of scleractinian corals belonging to 18 genera and 11 families were observed. We found a surprising pattern in the alpha diversity with greater values in the MPAs in the case of richness, with an average of 12 species. However, in the case of the N1 or N2 of Hill's numbers (based on a major weight for species with more cover and equivalent to Shannon and Simpson diversity respectively) a greater diversity was found in the unprotected sites (Fig. 5a–c). This shows the relevance of rare coral species in the protected sites, of which some are reef-building species such as *Acropora cervicornis* and *Orbicella annularis.*

On the basis of analysis of the local contribution to beta diversity (Fig. 5d), the most unique sites in terms of species composition are the Coralina, La Pared, and Cayo Ratón, MPAs that contribute to more than 50% of the total variation in the species composition. It is interesting that the Coralina Reef stands out for its high uniqueness and different species composition (p < 0.05) given the presence of the species *Orbicella annularis,* as this was the only site in which it was found; it is also the site with greatest *Dendrogyra cylindrus* cover.

Results of the analysis of EDGE index at site level showed that the protected site La Pared provides the largest ratio of evolutionary history and protection to threatened species. It has high coral cover and is dominated by the species *Orbicella faveolata.* Additionally, it is the only site where *Acropora cervicornis* is present. However, other protected reefs such as Atlantic Princess, Dominicus Reef, Cayo Ratón and El Peñón also have high EDGE index values. These MPAs protect a considerable percentage of the cover of species from the *Orbicella* genus, and they also have species such as *Montastraea cavernosa* and *Dendrogyra cylindrus,* which have high EDGE values. It is important to point out that high values of EDGE index were found at MPAs, sites that have a greater coral cover (Fig. 5e).

We found a significant difference in species composition between sites (PERMANOVA, Pseudo $F_{(12,65)}$ = 6.08, R^2 = 0.53 and permuted P = 0.001), even when NMDS ordination showed that most of the MPAs were clustered; however, at the Coralina site, composition exhibited important differences from the other sites (Fig. 6). Different species were relevant in the differentiation between sites highlighting some of them as: *Orbicella faveolata*, *Pseudodiploria strigosa*, *Diploria labyrinthiformis*, *Siderastrea siderea*, *Porites porites* and *Porites divaricata* (SIMPER, permutated P < 0.05). Some rare coral species were observed only at one site: *Orbicella annularis* (La Coralina); *Manicina areolata* (BC1); *Eusmilia fastigiata* (La Pared); *Acropora cervicornis* (La Pared); *Helioseris cucullata* (Punta Cacón); and *Siderastrea radians* (Punta Cacón) (Supplementary Figure S1). In the unprotected sites dominant species were *Pseudodiploria strigosa*, *Stephanocoenia intersepta*, *Agaricia agaricites*, as well as *P. astreoides, Meandrina meandrites,* and *O. faveolata* (Supplementary Figure S1). Within the MPAs the dominant species were *O. faveolata*, followed by *A. agaricites*, which were found in all sites (Supplementary Figure S1). Other dominant species in MPAs were *Orbicella* species complex and *Porites porites* (Supplementary Figure S1).

Agaricia agaricites and *Orbicella faveolata* species were recorded in all the sites and were the main species in Pa, AP, Pe, PC, and BC2 reefs. *Orbicella annularis* was present only in Coralina and dominated the reef, while *O. franksi* dominated the Dominicus Reef and *Porites porites* dominated at Cayo Ratón. At the unprotected sites, *Pseudodiploria strigosa* contributed to the greatest percentage at BC1, BC3, and BC5, while *Stephanocoenia intersepta* did so in BC4 and *Meandrina meandrites* in BC6. Based
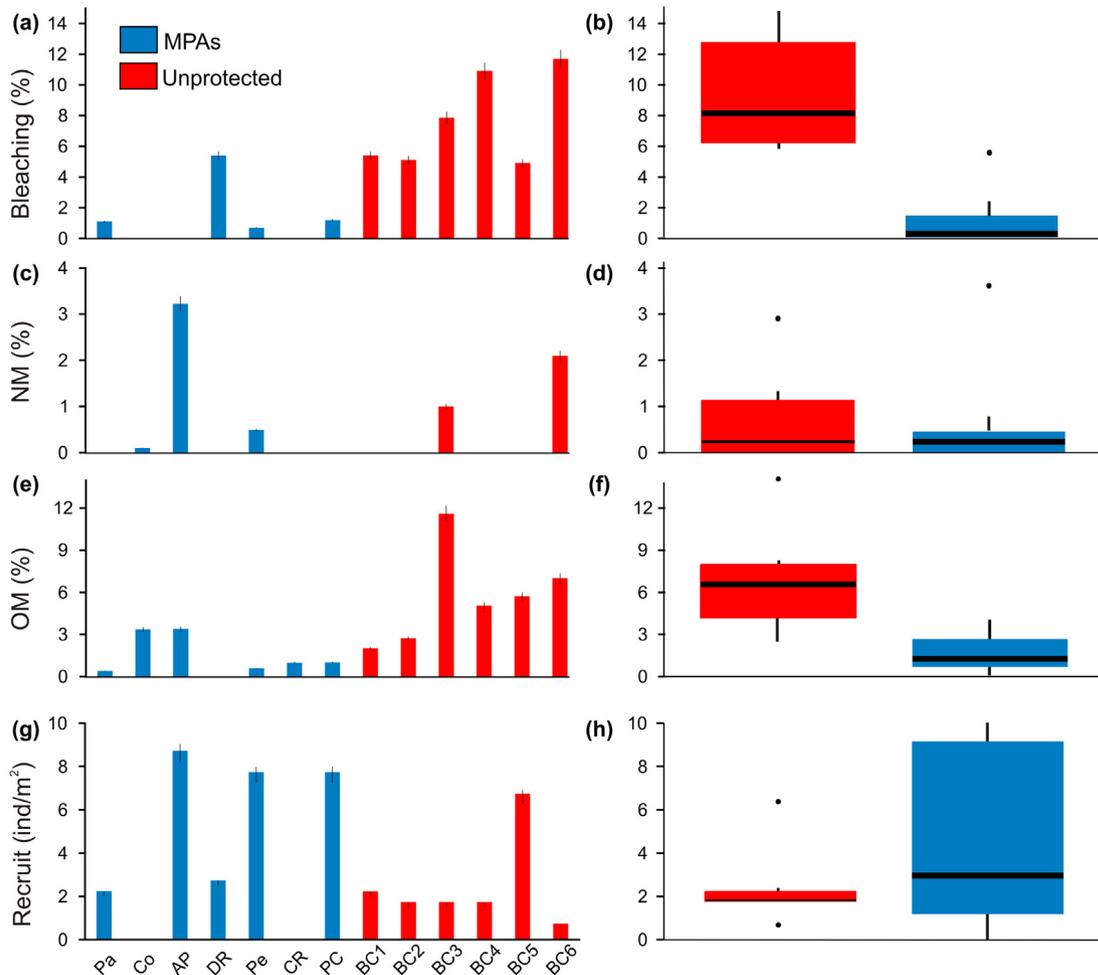
Fig. 4. Bleaching, mortality, and coral recruitment; (a) Relative proportion of coral bleaching by site, (b) coral bleaching %, (c) NM = new mortality % by site, (d) NM = new mortality %, (e) OM = old mortality % by site, (f) OM = old mortality %, (g) Recruits density/m² by site and (h) Recruits density/m². (right side figures are arranged by MPA status unprotected) (mean ± SE).
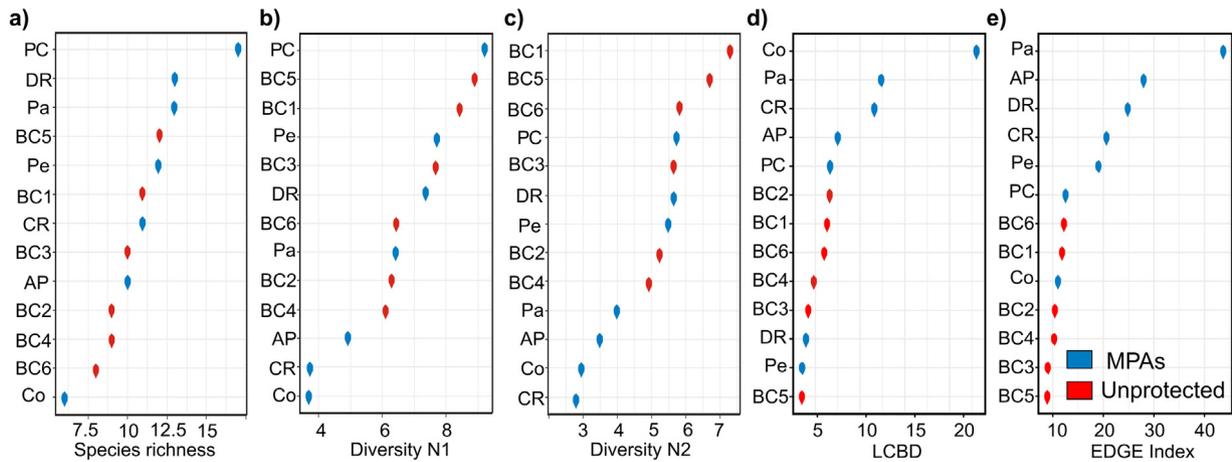
Fig. 5. (a) Species richness, (b) N_1 of Hill diversity, (c) N_2 of Hill diversity, (d) local contribution of Beta diversity (LCBD) and (e) EDGE index.

on the arrangement of coral species composition (Fig. 6), all the MPAs presented a differentiation from the unprotected sites, with the exception of Cayo Ratón were a composition similar to the BC site was found. This showed that the composition of the MPAs was primarily dominated by coral species with high structural complexity in comparison to the BC sites.

4. Discussion

Despite the alarming ecological condition of coral reefs in the Caribbean region (Jackson et al., 2014), our results show positive reef conditions in the SE Dominican Republic's MPA network. Live coral cover is higher (35 ± 5.8%) than in unprotected sites (12 ± 2%), and other reefs of the wider Caribbean (mean 17%)
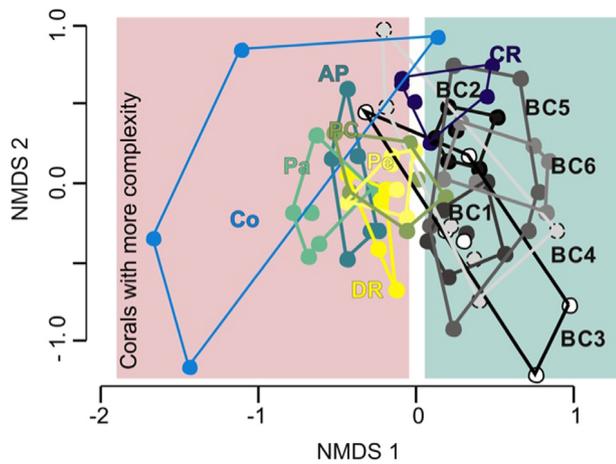
Fig. 6. Non-metric multidimensional scaling (NMDS) for coral species composition. Table 1 shows site codes and protection category.

exemplified by Jackson et al. (2014). Coral cover in this group of MPAs is similar to that observed in the Caribbean more than two decades ago (Gardner et al., 2003; Arias-González et al., 2017). The percentage of coral cover observed in southeastern Dominican in this study has increased by average of 20% over the reported baseline recorded at comparable sites in 1996 by Chiappone (2001). This was observed in the reefs visited during both studies, where the Dominicus Reef showed an improvement of coral cover from 20% to 37%; El Peñón from 11% to 31% and Punta Cacón from 11% to 26% in the baseline presented by Chiappone (2001) and our present study respectively. The highest live coral cover was observed at six MPA sites which agrees with the results of other studies in small MPAs demonstrating their benefit (Bonaldo et al., 2017). They are also consistent with reduced impacts as a result of protection status, like in Australia's Great Barrier Reef (Myers and Ambrose, 2009). However, at PBNM (Coralina), macroalgae dominated ($61 \pm 5.4\%$) and the lowest coral cover ($13 \pm 4.3\%$) was observed in this protected site. This could be mainly associated with local stress factors such as high wave and hurricane exposure and, a constant flow of boats and visitors, causing direct physical injuries to coral colonies. Besides, Bayahibe urban area is a short distance away (<500 m), which makes this Natural Monument vulnerable to dissolved nutrients and sediments. This condition is also notable at our unprotected sites studies, which have low live coral cover, and coincide with the values recorded for the same area by Chiappone (2001) with values lower than 10% in the two sites surveyed in Boca Chica in 1997. The phase shift reported at other Caribbean reefs (Jackson et al., 2014; Arias-González et al., 2017), has probably also occurred in this place, where macroalgae now dominates associated benthic substrate, a process recently linked to nutrient and pollution flushes which promote excessive proliferation of these organisms (Russ et al., 2015). Other studies on water quality parameters, such as suspended particles, heavy metals, nitrogen, and phosphorus, have found high values that correlate with negative impacts on coral larvae development, calcification, tissue growth and survival (Maynard et al., 2010). Precisely in the bay of Boca Chica there are physical and environmental problems associated with the rapid urbanization of the coastal area with direct impacts on water quality. Marine and coastal ecosystems, including coral reefs, are exposed to a system of solid waste collection and wastewater treatment that has surpassed the capacity of the municipality. For example, the wastewater treatment plant was built for an estimated population of 25 000 people and today more than 140 000 live in the area. Treated

waste water is discharged directly into the underground system and approximately 50% of sewage from the municipality goes into coral reefs (CORAABAO, 2016).

Other benthic components such as macroalgae and abiotic substrate are lower at MPAs (27 and 16%), along with indicators of coral bleaching relative to proportion ($<1\%$) and old mortality ($<1\%$). These findings agree with other studies, which emphasize that MPA networks reduce local impacts and improve reef condition, including scleractinian corals (Stockwell et al., 2009; Selig and Bruno, 2010; Mumby and Harborne, 2010; Lamb et al., 2015; Mellin et al., 2016).

Overall, we found that MPAs may have a positive impact on reef conditions individually and collectively, as they have more coral cover and better health indicators. We found relative positive changes over time when compared to data from 1997 collected by Chiaponne in reefs inside/outside MPAs. Even if Boca Chica has naturally lower in coral cover, it did not improve during this timeframe but the MPA sites did. These results may reflect the relatively low intensity of human activities at MPA zones in contrast to unprotected sites with more pronounced activities used for a wide variety of purposes and associated to urbanization and pollution.

Although most of the MPAs in this study have absent or inadequate budget capacity, with the exception of the CNP (below optimum) and absent or inadequate staff capacity (number/quality of staff (on-site), local management has influence in the region, for example, NGOs, local communities and non-state actors participate in management processes (Cortés-Useche et al., 2017). These results coincide with the work developed by Gill et al. (2017), where it is highlighted that many of the implemented MPAs did not reach the minimum thresholds for effective and equitable management processes, including the MPAs of the Caribbean region.

Local management activities have proven to be successful in other islands along the 700-km eastern Caribbean archipelago, improving the resilience of coral reef systems (Steneck et al., 2018). Some potential tools promoting positive conditions in the SE MPAs include the incorporation of local management measures; particularly important is the permanent closure of fishing activities and boat transit in the Catuano Canal (since 2009) in CNP, where Cayo Ratón reef is located. This reef is characterized by geographic isolation at the East end of Saona Island, very close to other marine ecosystems such as mangroves, seagrass beds and beaches (Chiappone, 2001). The relatively early implementation of MPAs like CNP (1975) and NMIC (1995), may explain that positive effects of protected areas are linked to the number of years they are under protection (Edgar et al., 2014). In addition, dive centres, local communities, and NGOs have been actively involved in installing mooring buoys and signals at Pa, AP, DR, Pe and PC sites, and are consistently surveilling the area. The low or closed dive activities within MPA sites may explain the effectiveness in reducing direct impacts on coral colonies (Edgar et al., 2014; Aswani et al., 2015). Resolution No. 023−17 (2017) has been instated in this country, which declares the closure of capture and marketing of all species of sharks, rays, parrot/doctor fish and urchins living in territorial waters, as well as trade of derivative products, including exports and imports (Cortés-Useche et al., 2017).

Based on the results of the study, we conclude that the region of SE Dominican Republic did not suffer massive bleaching or mortality. The percentage of these conditions in corals was relatively low in all studied sites ($<12\%$). This is largely due to the low heat stress presented in the study area in 2015 (Supplementary Figure S2; Muñiz-Castillo et al., 2019). Although 2015 was one of the most important heat-stress events in other regions of the Caribbean, such as Florida, the Gulf of Mexico and the Mesoamerican Reef System, this last heat-stress event did not impact the

reefs of the Southeast of the Dominican Republic. These reefs however, are also located in one of the regions with the least exposure to heat stress in the wider Caribbean (Supplementary Figure S2; Muñiz-Castillo et al., 2019). In the reefs of the Southeast of the Dominican Republic no considerable impact of the last global bleaching event was observed, as it was observed in other parts of the planet such as Australia (Hughes et al., 2017) and Florida (Gintert et al., 2018).

Coral recruitment is a factor influencing biodiversity and bioconstruction of coral reefs. In this study, MPAs exhibited greater recruitment densities (mean = 4 ind/m^2) when compared to the BC area (2 ind/m^2). However, we found high variation and no significant difference between the two areas, probably because of the high variability of coral recruitment, a fact that has been demonstrated by other studies (Luter et al., 2016). The observed recruitment rates in MPAs during this study (4 ind/m^2) were greater than recorded by Chiappone (2001) in the area (2 ind/m^2) in 1996 and coincide to coral dominated state for these reefs (Alcolado and Durán, 2011). However, recruitment values are low as compared to other studies in the Caribbean region (7–14 ind/m^2) (Vermeij et al., 2011; Steneck et al., 2015). Our study found high values of crustose coralline algae (CCA) at both MPA sites and the BC area (13% and 16%), which were more than values from other reports in the same region in the Dominican Republic (1% and 2%) (Chiappone, 2001). However, data from this study could not demonstrate the positive effects of CCA on coral recruitment. This could be associated with the negative effects caused by macroalgae, other invertebrates (e.g. sponges) and high sedimentation rates (Torres et al., 2001). Additionally, the cyanobacteria present in the SE reefs, limits recruitment success (Arnold and Steneck, 2011).

Coral diversity analysis shows that live coral cover is a key variable in sustaining coral reef biodiversity (Bellwood and Hughes, 2001; Arias-González et al., 2008). Sites with high coral cover and high diversity indicate healthy reefs (Anthony et al., 2015; Aswani et al., 2015). In our case study we found that MPAs generally present more species richness, but less diversity (Hill N1 and N2 numbers) than unprotected sites. This highlights the relevance of rare or less abundant species in the case of MPAs, which contribute considerably to the richness of protected sites. Comparing the richness data obtained in this work with those recorded by Chiappone (2001), we found a greater number of species at present during our observation. At the Dominicus Reef we found a richness of 13 species when compared to the 10 previously recorded, at El Peñón we recorded 12 species as opposed to the 9 recorded earlier. However, this increase in species richness may be due to an effect of the use of scientific nomenclature, where some species such as the *Orbicella* species complex were considered a single species in earlier studies (*Orbicella annularis*), for example many authors considered them to be comprised of three morphotypes or sibling species (Knowlton, 1992) as mentioned by Chiappone (2001).

Recent studies suggest that protected reefs have greater β-diversity, and spatially heterogeneous communities (Mellin et al., 2014). It is important to highlight that greater biodiversity could maximize functional ecosystem redundancy (Thibaut et al., 2012; Anderson et al., 2013). In this study we observed that the combination of some of these MPA zones protects more than 50% of diversity variation and fosters the protection of coral evolutionary history. This marks the relevance of protecting species diversity and phylogenetic diversity offered by MPAs as a network of MPAs and shows great relevance for the conservation of tropical Atlantic reefs (Mouillot et al., 2016). Caribbean corals are being impacted by multiple stressors, some global such as constant exposure to heat stress and its increasing trend in the Caribbean region (Muñiz-Castillo et al., 2019), as well as other local impacts such as pollution and coastal development (Arias-González et al., 2016, 2017), adding the devastating regional impact that they are suffering due to the recent outbreak of the stony coral tissue loss disease (SCTLD) (Precht et al., 2016; AGRRA, 2019). This decline in the main formers of coral reefs calls for a prioritization approach to conservation with special attention to the ecological characteristics of coral assemblages.

In the MPAs, *Orbicella* species complex is a major contributor to reef construction (>46% of the relative coral cover). The pattern of dominance of *Orbicella* species complex observed in these MPAs coincides with the ones described for the same area (Southeastern) by Chiappone (2001) between 1994 and 1997. These species of the *Orbicella* complex make a significant contribution to living coral cover, have high rates of survival, and are highly competitive (Sorokin, 1995; Brown, 1997). *Acropora* species on the other hand were marginal, but large patches of *A. cervicornis* corals were found at La Pared reef; this species is seriously threatened and its populations in the Caribbean are reduced (Nyström et al., 2000). These results highlight the importance of conserving lineages of coral species classified in the Top-10 species with a high grade of evolutionary distinctiveness and that are at a risk of extinction (Huang, 2012; Curnick et al., 2015). Protecting reefs dominated by reef-building *Orbicella* species complex, as well as reefs with seriously threatened fast-growing *Acropora* species, is a key priority to sustain coral reef ecological processes (Mumby et al., 2008; Alvarez-Filip et al., 2013; Rodríguez-Zaragoza and Arias-González, 2015).

According to Chiappone (2001), a majority of the coral cover in most sites surveyed within the area between 1994 and 1997 (Dominicus Reef, El Peñón and Boca Chica) comprised of *O. annularis, M. cavernosa, Agaricia agaricites*, and *Siderastrea siderea*. In our study *Orbicella annularis* was present only in Coralina and small colonies of *Pseudodiploria strigosa* (brain) and *Siderastrea siderea* (semi-spherical) provide the largest contribution in the unprotected sites. This seems to indicate a change in submarine seascape over time, i.e., a degraded environment is dominated by species of smaller size and less structural complexity (Darling et al., 2012; Rodríguez-Zaragoza and Arias-González, 2015; Newman et al., 2015). However, these results compared with data from more than 20 years ago, show that MPAs not only have higher live coral coverage but also a species composition that is still dominated by reef-building corals. This is despite the presence of coral species with a high degree of evolutionary distinctiveness and that are in danger of extinction. Recent studies emphasize that coral composition and diversity are changing in the Caribbean; species of genus *Agaricia* spp. and *Porites* spp. tend to dominate the seascape, reducing the complexity of the habitat and modifying ecosystem functions (Alvarez-Filip et al., 2013; Perry et al., 2015).

One of the main contributions of this work is the use of indicators based on the diversity and evolutionary history provided by each of the species. On one hand, the use of diversity is important for decision-making, which can be based on the condition and structure of coral reefs, instead of considering only species richness. On the other hand, the analysis of the spatial variation of the community through local contribution to beta diversity LCBD is an indicator of the uniqueness of the composition of species present in the sites; in this sense, large values of the LCBD highlight sites with high conservation potential or potentially degraded, where unique or rare species may occur (Legendre and De Cáceres, 2013; Mellin et al., 2014). Coralina Reef has a very particular composition, where the two species that dominate have low abundance than in the rest of the evaluated sites. Although Coralina has poor reef conditions because of low coral cover, its contribution to regional diversity is remarkable due to its high LCBD values. Other sites with a significant contribution are La Pared in CINM and Cayo Ratón in CNP, both

with high relevance for conservation in the region as they are in excellent reef condition and they contribute significantly to regional diversity.

5. Conclusion

This is the first study demonstrating that coral reefs, which are a part of the MPA network in the SE Dominican Republic, have high coral cover, and favourable coral reef condition indicators. This study emphasizes on hot spots, promoting effective local management tools, preserving untouched and isolated reefs (Cayo Ratón), protecting exposed reefs (La Pared y Atlantic Princess), and reducing reef threats (Dominicus Reef, Peñón and Punta Cacón). Restoration of affected reefs by local stressors, such as at La Coralina in PBNM, should also be considered due to its great uniqueness and species composition, such as the presence of *Orbicella annularis* and a higher coverage of *Dendrogyra cylindrus.* Current strategies aim to identify and protect disturbance resistant and resilient reefs and to ensure the protection of coral builders in the tropical Atlantic. Some of the Dominican Republic's SE MPAs have been established since 1975 and are enforced by local participation, through fishermen, divers, NGOs, businessmen and committed government authorities that have supported the resource management process for several years, exerting control and permanent surveillance in the area. Our findings indicate that local reef management should continue because the benefits of MPAs may increase with efficient management. These reefs could offer a good model of coral reef management in the Caribbean, considering local management scheme involving long-term ecological and economic synergisms could provide the basis for a future management model directly benefiting both reefs condition and society.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2019.100893.

References

Agardy, T., di Sciara, G.N., Christie, P., 2011. Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar. Policy 35, 226–232. http://dx.doi.org/10.1016/j.marpol.2010.10.006.

Alcolado, P.M., Durán, A., 2011. Sistema de escalas para la clasificación y puntaje de condición del bentos e ictiofauna de arrecifes coralinos de Cuba y del Gran Caribe. Ser. Oceanol. 8, 25–29.

Alvarez-Filip, L., Carricart-Ganivet, J.P., Horta-Puga, G., Iglesias-Prieto, R., 2013. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. Sci. Rep. 3 (3486), http://dx.doi.org/10.1038/srep03486.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. http://dx.doi.org/10.1046/j.1442-9993.2001.01070.x.

Anderson, S.C., Cooper, A.B., Dulvy, N.K., 2013. Ecological prophets: Quantifying metapopulation portfolio effects. Methods Ecol. Evol. 4, 971–981. http://dx.doi.org/10.1111/2041-210X.12093.

Anthony, K.R.N., Marshall, P.a., Abdulla, A., Beeden, R., Bergh, C., Black, R., Eakin, C.M., Game, E.T., Gooch, M., Graham, N.a.J., Green, A., Heron, S.F., van Hooidonk, R., Knowland, C., Mangubhai, S., Marshall, N., Maynard, J.a., Mcginnity, P., Mcleod, E., Mumby, P.J., Nystr??m, M., Obura, D., Oliver, J., Possingham, H.P., Pressey, R.L., Rowlands, G.P., Tamelander, J., Wachenfeld, D., Wear, S., 2015. Operationalizing resilience for adaptive coral reef management under global environmental change. Glob. Chang. Biol. 21, 48–61. http://dx.doi.org/10.1111/gcb.12700.

Arias-González, J.E., Fung, T., Seymour, R.M., Garza-Pérez, J.R., Acosta-González, G., Bozec, Y.M., Johnson, C.R., 2017. A coral-algal phase shift in Mesoamerica not driven by changes in herbivorous fish abundance. PLoS One 12, e0174855. http://dx.doi.org/10.1371/journal.pone.0174855.

Arias-González, J.E., Legendre, P., Rodríguez-Zaragoza, F.A., 2008. Scaling up beta diversity on Caribbean coral reefs. J. Exp. Mar. Bio. Ecol. 366, 28–36. http://dx.doi.org/10.1016/j.jembe.2008.07.035.

Arias-González, J.E., Rivera-Sosa, A., Zaldívar-Rae, J., Alva-Basurto, C., Cortés-Useche, C., 2016. The animal forest and its socio-ecological connections to land and coastal ecosystems. In: Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds.), Marine Animal Forests. Springer, Switzerland, http://dx.doi.org/10.1007/978-3-319-17001-5_33-1.

Arnold, S.N., Steneck, R.S., 2011. Settling into an increasingly hostile world: The rapidly closing "recruitment window" for corals. PLoS One 6, http://dx.doi.org/10.1371/journal.pone.0028681.

Aronson, R., Bruckner, A., Moore, J., Precht, B., Weil, E., 2008. Acropora cervicornis. The IUCN Red List of Threatened Species 2008: e.T133381A3716457. Available from http://dx.doi.org/10.2005/UICN.UK.2008.RLTS.T133381A3716457.en.

Aswani, S., Mumby, P.J., Baker, A.C., Christie, P., McCook, L.J., Steneck, R.S., Richmond, R.H., 2015. Scientific frontiers in the management of coral reefs. Front. Mar. Sci. 2 (50), http://dx.doi.org/10.3389/fmars.2015.00050.

Atlantic and Gulf Rapid Reef Assessment (AGRRA), 2019. Program. stony coral tissue loss disease. at http://www.agrra.org/coral-disease-outbreak/.

Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proc. Natl. Acad. Sci. 107, 18256–18261. http://dx.doi.org/10.1073/pnas.0908012107.

Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science (80-.) 292, 1532–1535. http://dx.doi.org/10.1126/science.1058635.

Corporación del Acueducto y Alcantarillado de Boca Chica (CORAABAO), 2016. Plan municipal de desarrollo boca chica. At http://www.coraabo.gob.do/index.php/comunicaciones/estadistica.

Bonaldo, R.M., Pires, M.M., Guimarã, .P.R., Hoey, A.S., Hay, M.E., 2017. Small marine protected areas in Fiji provide refuge for reef fish assemblages, feeding groups, and corals. PLoS One 12 (1), http://dx.doi.org/10.1371/journal.pone.0170638.

Brown, B.E., 1997. Disturbances to reefs in recent times. In: Life and Death of Coral Reefs. pp. 354–379.

Burke, L.M., Maidens, J., 2004. Coral Reefs at Risk in the Caribbean. World Resources Institute, Washington, DC, p. 80.

Burke, L.M., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at Risk Revisited. World Resources Institute, Washington, DC.

Calle-Triviño, J., Cortés-Useche, C., Sellares-Blasco, R.I., Arias-González, J.E., 2018. Assisted fertilization of threatened Staghorn Coral to complement the restoration of nurseries in Southeastern Dominican Republic. Reg. Stud. Mar. Sci. 18, 129–134. https://doi.org/10.1016/j.rsma.2018.02.002.

Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Wood, E., 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321 (5888), 560–563. http://dx.doi.org/10.1126/science.1159196.

Chambers, J.M., Freeny, A., Heiberger, R.M., 1992. Analysis of variance; designed experiments. In: Chambers, J.M., Hastie, T.J. (Eds.), Statistical Models.

Chiappone, M., 2001. Coral reef conservation in marine protected areas a case study of parque nacional del este, the nature conservancy.

Cinner, J.E., Huchery, C., MacNeil, M.A., Graham, N.a.J., McClanahan, T.R., Maina, J., Maire, E., Kittinger, J.N., Hicks, C.C., Mora, C., Allison, E.H., D'Agata, S., Hoey, A., Feary, D.a., Crowder, L., Williams, I.D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G., Stuart-Smith, R.D., Sandin, S.a., Green, A.L., Hardt, M.J., Beger, M., Friedlander, A., Campbell, S.J., Holmes, K.E., Wilson, S.K., Brokovich, E., Brooks, A.J., Cruz-Motta, J.J., Booth, D.J., Chabanet, P., Gough, C., Tupper, M., Ferse, S.C.a., Sumaila, U.R., Mouillot, D., 2016. Bright spots among the world's coral reefs. Nature 1–17. http://dx.doi.org/10.1038/nature18607.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. http://dx.doi.org/10.1111/j.1442-9993.1993.tb00438.x.

Claudet, J. (Ed.), 2011. Marine Protected Areas. Cambridge University Press, http://dx.doi.org/10.1017/CBO9781139049382.

Cortés-Useche, C., Sellares, R.I., Calle-Triviño, J., Baéz, A., Arias-González, J.E., 2017. Conservation of coral reef ecosystems of the southeastern dominican Republic (abstract no. 013). In: Paper Presented at 28th International Congress for Conservation Biology. Cartagena, Colombia, July 2017.

Cox, Courtney, Valdivia, A., McField, Melanie D., Castillo, K., Bruno, J.F., 2017. Establishment of marine protected areas alone does not restore coral reef communities in Belize. Mar. Ecol. Prog. Ser. 563, 65–79, https://doi.org/10.3354/meps11984.

Currnick, D.J., Head, C.E.I., Huang, D., Crabbe, M.J.C., Gollock, M., Hoeksema, B.W., Johnson, K.G., Jones, R., Koldewey, H.J., Obura, D.O., Rosen, B.R., Smith, D.J., Taylor, M.L., Turner, J.R., Wren, S., Redding, D.W., 2015. Setting evolutionary-based conservation priorities for a phylogenetically data-poor taxonomic group (scleractinia). Animal Conserv. 18, 303–312. http://dx.doi.org/10.1111/acv.12185.

Darling, E.S., Alvarez-Filip, L., Oliver, T.A., Mcclanahan, T.R., Cote, I.M., 2012. Evaluating life-history strategies of reef corals from species traits. Ecol. Lett. 15, 1378–1386. http://dx.doi.org/10.1111/j.1461-0248.2012.01861.x.

Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Legendre, P., Wagner, H.H., 2016. Adespatial: multivariate multiscale spatial analysis. R Packag. version.

Eastwood, E.K., Clary, D.G., Melnick, D.J., 2017. Coral reef health and management on the verge of a tourism boom: A case study from Miches, Dominican Republic. Ocean Coast. Manag. 138, 192–204. http://dx.doi.org/10.1016/j.ocecoaman.2017.01.023.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.a., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.a., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220. http://dx.doi.org/10.1038/nature13022.

Gardner, T.a., Côté, I.M., Gill, J.a., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. Science (80-.) 301, 958–960. http://dx.doi.org/10.1126/science.1086050.

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craige, I., Darling, E.S., Free, C.M., Geldman, J., Holst, S., Jenses, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.M., Thomas, H., Whitmee, S., Woodley, S., Fox, H., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature 543 (7647).

Gintert, B.E., Manzello, D.P., Enochs, I.C., Kolodziej, G., Carlton, R., Gleason, A.C.R., Gracias, N., 2018. Marked annual coral bleaching resilience of an inshore patch reef in the Florida Keys: A nugget of hope, aberrance, or last man standing?. Coral Reefs 1–15. http://dx.doi.org/10.1007/s00338-018-1678-x.

Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C., Jennings, S., ..., Sheppard, C.R.C., 2008. Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS One 3 (8), e3039, Retrieved from https://doi.org/10.1371/journal.pone.0003039.

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P., Robinson, J., 2006. Dynamic fragility of oceanic coral reef ecosystems. Proc. Natl. Acad. Sci. 103, 8425–8429. http://dx.doi.org/10.1073/pnas.0600693103.

Heery, E.C., Hoeksema, B.W., Browne, N.K., Reimer, J.D., Ang, P.O., Huang, D., … Todd, P.A., 2018. Urban coral reefs: Degradation and resilience of hard coral assemblages in coastal cities of East and Southeast Asia. Mar. Pollut. Bull. 135, 654–681. http://dx.doi.org/10.1016/j.marpolbul.2018.07.041.

Hill, M.O., 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54, 427–432. http://dx.doi.org/10.2307/1934352.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, a.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, a.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., Hatziolos, M.E., 2007. Coral reefs under rapid climate change and ocean acidification. Science (80-.) http://dx.doi.org/10.1126/science.1152509.

Hollander, M.A., Wolfe, D., Chicken, E., 2015. The one-way layout. In: Nonparametric Statistical Methods. pp. 202–288. http://dx.doi.org/10.1002/9781119196037.ch6.

Huang, D., 2012. Threatened reef corals of the world. PLoS One 7, e34459. http://dx.doi.org/10.1371/journal.pone.0034459.

Hughes, T.P., Baird, H.a., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933. http://dx.doi.org/10.1126/science.1085046.

Hughes, T.P., Kerry, J.T., Álvarez Noriega, M., Álvarez Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M., Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M., Figueira, W.F.,

Gilmour, J.P., Harrison, H.B., Heron, S.F., Hoey, A.S., Hobbs, J.P.A., Hoogenboom, M.O., Kennedy, E.V., Kuo, C.Y., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm, H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T., Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L., Wilson, S.K., 2017. Global warming and recurrent mass bleaching of corals. Nature 543, 373–377. http://dx.doi.org/10.1038/nature21707.

Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C., Baillie, J.E.M., 2007. Mammals on the EDGE: Conservation priorities based on threat and phylogeny. PLoS One 2 (3), http://dx.doi.org/10.1371/journal.pone.0000296.

IUNC, 2017. IUCN red list of threatened species. In: International Union for Conservation of Nature and Natural Resources. http://www.iucnredlist.org. Accessed 25.03.18.

Jackson, J., Donovan, M., Cramer, K., Lam, V., 2014. Status and trends of Caribbean coral reefs: 1970-2012. In: Global Coral Reef Monitoring Network. IUCN, Gland, Switzerland.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439. http://dx.doi.org/10.1890/06-1736.1.

Knowlton, N., 1992. Thresholds and multiple stable states in coral reef community dynamics. Integr. Comp. Biol. 32 (6).

Kramer, P.A., 2003. Synthesis of coral reef health indicators for the western Atlantic: Results of the AGRRA program (1997-2000). Atoll Res. Bull. 496, 1–58.

Lamb, J.B., Williamson, D.H., Russ, G.R., Willis, B.L., 2015. Protected areas mitigate diseases of reef-building corals by reducing damage from fishing. Ecology 96, 2555–2567. http://dx.doi.org/10.1890/14-1952.1.

Lang, J.C., Marks, K.W., Kramer, P.A., Kramer, P.R., Ginsburg, R.N., 2010. AGRRA Protocols Version 5.4. Atlantic and Gulf Rapid Reef Assessment. Miami, FL. USA.

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. http://dx.doi.org/10.1111/ele.12141.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280. http://dx.doi.org/10.1007/s004420100716.

Legendre, P., Legendre, L.F., 2012. Numerical Ecology, Vol. 24, third ed. Elsevier, Chicago.

Luter, H.M., Duckworth, A.R., Wolff, C.W., Evans-Illidge, E., Whalan, S., 2016. Recruitment variability of coral reef sessile communities of the far north great barrier reef. PLoS One 11, e0153184. http://dx.doi.org/10.1371/journal.pone.0153184.

Marcon, E., Hérault, B., 2015. Entropart : An r package to measure and partition diversity. J. Stat. Softw. 67, 1–26. http://dx.doi.org/10.18637/jss.v067.i08.

Maynard, J.A., Marshall, P.A., Johnson, J.E., Harman, S., 2010. Building resilience into practical conservation: Identifying local management responses to global climate change in the southern great barrier reef. Coral Reefs 29, 381–391. http://dx.doi.org/10.1007/s00338-010-0603-8.

McClanahan, T.R., Donner, S.D., Maynard, J.a., MacNeil, M.A., Graham, N.a.J., Maina, J., Baker, A.C., Alemu, I., J.B, Beger, M., Campbell, S.J., Darling, E.S., Eakin, C.M., Heron, S.F., Jupiter, S.D., Lundquist, C.J., McLeod, E., Mumby, P.J., Paddack, M.J., Selig, E.R., van Woesik, R., 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. PLoS One 7, e42884. http://dx.doi.org/10.1371/journal.pone.0042884.

McClanahan, T.R., Marnane, M.J., Cinner, J.E., Kiene, W.E., 2006. A comparison of marine protected areas and alternative approaches to coral-reef management. Curr. Biol. 16, 1408–1413. http://dx.doi.org/10.1016/j.cub.2006.05.062.

McCook, L.J., Ayling, T., Cappo, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B., Marsh, H., Mills, M., Molloy, F.J., Pitcher, C.R., Pressey, R.L., Russ, G.R., Sutton, S., Sweatman, H., Tobin, R., Wachenfeld, D.R., Williamson, D.H., 2010. Adaptive management of the great barrier reef: A globally significant demonstration of the benefits of networks of marine reserves. Proc. Natl. Acad. Sci. 107, 18278–18285. http://dx.doi.org/10.1073/pnas.0909335107.

Mellin, C., Aaron Macneil, M., Cheal, A.J., Emslie, M.J., Julian Caley, M., 2016. Marine protected areas increase resilience among coral reef communities. Ecol. Lett. 19, 629–637. http://dx.doi.org/10.1111/ele.12598.

Mellin, C., Bradshaw, C.J.A., Fordham, D.A., Caley, M.J., 2014. Strong but opposing -diversity-stability relationships in coral reef fish communities. Proc. R. Soc. B Biol. Sci. 281, 20131993. http://dx.doi.org/10.1098/rspb.2013.1993.

Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233. http://dx.doi.org/10.1016/S0921-8009(99)00009-9.

Mora, C., 2008. A clear human footprint in the coral reefs of the Caribbean. Proc. R. Soc. B Biol. Sci. 275, 767–773. http://dx.doi.org/10.1098/rspb.2007.1472.

Mora, C., Andréfouët, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J., Gaston, K.J., Myers, R.a., 2006. Coral reefs and the global network of marine protected areas. Science (80-.) http://dx.doi.org/10.1126/science.1125295.

Mora, C., Graham, N.a.J., Nyström, M., 2016. Ecological limitations to the resilience of coral reefs. Coral Reefs http://dx.doi.org/10.1007/s00338-016-1479-z.

Mouillot, D., Parravicini, V., Bellwood, D.R., Leprieur, F., Huang, D., Cowman, P.F., Albouy, C., Hughes, T.P., Thuiller, W., Guilhaumon, F., 2016. Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. Nature Commun. 7 (10359), http://dx.doi.org/10.1038/ncomms10359.

Muñiz-Castillo, A.I., Rivera-Sosa, A., Chollett, I., Eakin, C.M., Andrade-Gómez, L., McField, M., Arias-González, J.E., 2019. Three decades of heat stress exposure in Caribbean coral reefs: a new regional delineation to enhance conservation. Sci. Rep. http://dx.doi.org/10.1038/s41598-019-47307-0.

Mumby, P.J., Broad, K., Brumbaugh, D.R., Dahlgren, C.P., Harborne, A.R., Hastings, A., Holmes, K.E., Kappel, C.V., Micheli, F., Sanchirico, J.N., 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conserv. Biol. 22, 941–951. http://dx.doi.org/10.1111/j.1523-1739.2008.00933.x.

Mumby, P.J., Harborne, A.R., 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS One 5 (1), http://dx.doi.org/10.1371/journal.pone.0008657.

Myers, M.R., Ambrose, R.F., 2009. Differences in benthic cover inside and outside marine protected areas on the Great Barrier reef: Influence of protection or disturbance history? Aquat. Conserv. Mar. Freshw. Ecosyst. 19, 736–747. http://dx.doi.org/10.1002/aqc.1053.

Newman, S.P., Meesters, E.H., Dryden, C.S., Williams, S.M., Sanchez, C., Mumby, P.J., Polunin, N.V.C., 2015. Reef flattening effects on total richness and species responses in the Caribbean. J. Anim. Ecol. 84, 1678–1689. http://dx.doi.org/10.1111/1365-2656.12429.

Nyström, M., C., Folke., F., Moberg., 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol Evol. 15, 413–417.

Oksanen, J., Blanchet, G.F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Wagner, H., 2016. Vegan: Community ecology package. R Packag. version.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.a., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R., Jackson, J.B.C., 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science (80-.) 301, 955–958. http://dx.doi.org/10.1126/science.1085706.

Perry, C.T., Steneck, R.S., Murphy, G.N., Kench, P.S., Edinger, E.N., Smithers, S.G., Mumby, P.J., 2015. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. Glob. Chang. Biol. 21, 1153–1164. http://dx.doi.org/10.1111/gcb.12792.

Porto-Hannes, I., Zubillaga, A.L., Shearer, T.L., Bastidas, C., Salazar, C., Coffroth, M.A., Szmant, A.M., 2015. Population structure of the corals orbicella faveolata and Acropora palmata in the Mesoamerican Barrier Reef System with comparisons over Caribbean basin-wide spatial scale. Mar. Biol. 162, 81–98. http://dx.doi.org/10.1007/s00227-014-2560-1.

Precht, W.F., Gintert, B.E., Robbart, M.L., Fura, R., Van Woesik, R., 2016. Unprecedented disease-related coral mortality in southeastern Florida. Sci. Rep. http://dx.doi.org/10.1038/srep31374.

R Core Team, 2016. R: A language and environment for statistical computing.

Reaka-Kulda, M.L., 1997. The global biodiversity of coral reefs: a comparison with rainforests. In: Reaka-Kulda, M.L., Wilson, D.E., Wilson, O.E. (Eds.), Biodiversity II: Understanding and Protecting Our Natural Resources. Joseph Henry/National Academy Press, Washington, DC, pp. 83–108.

Rodríguez-Zaragoza, F.a., Arias-González, J.E., 2015. Coral biodiversity and bioconstruction in the northern sector of the mesoamerican reef system. Front. Mar. Sci. 2, 1–16. http://dx.doi.org/10.3389/fmars.2015.00013.

Russ, G.R., Questel, S.L.A., Rizzari, J.R., Alcala, A.C., 2015. The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Mar. Biol. 162, 2029–2045. http://dx.doi.org/10.1007/s00227-015-2728-3.

Selig, E.R., Bruno, J.F., 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS One 5, http://dx.doi.org/10.1371/journal.pone.0009278.

SINAP, 2014. Sistema Nacional de áReas Protegidas, Base Legal, 2014. Ministerio de Medio Ambiente y Recursos Naturales, Santo Domingo, República Dominicana.

Sorokin, I.Y., 1995. Coral Reef Ecology, second ed. Springer Verlag, New York, NY.

Steneck, R.S., Arnold, S.N., de León, R., Rasher, D.B., 2015. Status and trends of bonaire's coral reefs in 2015: Slow but steady signs of resilence. p. 59.

Steneck, R.S., Mumby, P.J., Macdonald, C., Rasher, D.B., Stoyle, G., 2018. Attenuating effects of ecosystem management on coral reefs. Sci. Adv. 4, 1–12. http://dx.doi.org/10.1126/sciadv.aao5493.

Stockwell, B., Jadloc, C.R.L., Abesamis, R.A., Alcala, A.C., Russ, G.R., 2009. Trophic and benthic responses to no-take marine reserve protection in the Philippines. Mar. Ecol. Prog. Ser. 389, 1–15. http://dx.doi.org/10.3354/meps08150.

Thibaut, L.M., Connolly, S.R., Sweatman, H.P.A., 2012. Diversity and stability of herbivorous fishes on coral reefs. Ecology 93, 891–901. http://dx.doi.org/10.1890/11-1753.1.

Torres, R., Chiappone, M., Geraldes, F., Rodriguez, Y., Vega, M., 2001. Sedimentation as an important environmental influence on dominican Republic reefs. Bull. Mar. Sci. 69, 805–818.

Vermeij, M.J.A., Bakker, J., van der Hal, N., Bak, R.P.M., 2011. Juvenile coral abundance has decreased by more than 50% in only three decades on a small Caribbean Island. Diversity 3, 296–307. http://dx.doi.org/10.3390/d3030296.

Veron, J.E., 2000. Corals of the World. Australian Institute of Marine Science, Townsville.

Warton, D.I., Wright, S.T., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods Ecol. Evol. 3, 89–101. http://dx.doi.org/10.1111/j.2041-210X.2011.00127.x.

Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature http://dx.doi.org/10.1038/nature13947.

Wilkinson, C., 2008. Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre. Townsville, Australia.

Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice Hall, New Jersey.