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Research

Functional divergence from ecological baselines on Caribbean coral reefs

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Understanding how emergent ecological assemblages have diverged from natural states is fundamental in predicting future functioning and services of ecosystems. Coral reefs are of particular concern due to their high susceptibility to anthropogenic stressors. Yet, little is known about their pre-disturbance ranges of natural states, and most reports of decline are based on a limited number of sites and high levels of uncertainty. Here, we used a novel approach to estimate the physical functionality of reefs across marine ecoregions based on habitat suitability and morpho-functional traits for coral species. We calibrated ecological niche models for 49 reef-building corals of the Greater Caribbean based on occurrence records and environmental predictors, which we combined with species-specific functional coefficients derived from morpho-functional traits reflecting their contribution to the reef three-dimensional structure to estimate the reef functional potential (RFP). We then assessed the degree of divergence of western Caribbean reefs by comparing our physical functionality estimates against recent field data evaluations. We found spatial variability in RFP across the Caribbean, with the highest mean value in the western Caribbean and the lowest in areas with marginal environmental conditions. Hotspots of RFP exist along the coast of Belize and the southeast of Cuba. Overall, 84% of sites along the western Caribbean showed a substantial reduction in their physical functioning, with the highest reductions occurring within hotspots, implying that reefs displaying the greatest changes have high initial RFP. We conclude that combining niche models with species morpho-functional traits is a valuable and promising approach to estimate the large-scale functional potential of communities and the degree of change in the absence of ecological baselines. These findings have important implications and could be used to guide efforts to preserve coral reefs functionality and define priority conservation areas in the Caribbean.

Keywords: ecological niche models, functional traits, Maxent, species assemblages, stony corals, structural complexity



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Introduction

Ecosystem functioning and services largely depend upon the species combinations and traits that form biological communities (Mouillot et al. 2011). There is increasing evidence that environmental stress modifies the structure of these communities, but details on how functional traits of the resulting species combinations affect ecosystem functions are still uncertain (Funk et al. 2017). Trait-based approaches have a long history and are well established in ecological studies (Violle et al. 2007); nevertheless, their incorporation into ecological modelling is more recent (Zakharova et al. 2019). Overall, trait-based approaches incorporate any morphological or physiological trait measurable at the individual level, which indirectly affects organism performance (Violle et al. 2007). The use of functional traits thereby links an organism's performance to its functional role in populations, communities and ecosystems (Zakharova et al. 2019). The use of trait-based modelling approaches with emphasis on environmental gradients should therefore be more successful in providing general and predictable rules of a community's response to perturbations (McGill et al. 2006, Laughlin and Laughlin 2013, Mouillot et al. 2013, Scherrer et al. 2019). This is particularly relevant in the case of foundation species which, owing to their functional traits, create and define entire ecological communities or ecosystems, and whose loss can be severe for biodiversity and ecosystem services (Ellison et al. 2005).

In tropical shallow marine environments, reef-building corals are foundation species, and are the primary constructors of the physical three-dimensional structure by adding large amounts of calcium carbonate (Perry et al. 2012, Graham and Nash 2013). The physical functionality of reefs favors a high diversity of associated taxa through the provision of heterogeneous habitats that allow the regulation of ecological processes such as recruitment, competition and predation (Pratchett et al. 2008, Coker et al. 2009, Graham and Nash 2013).

Usually, the assessment of reef condition is based on estimations of total coral cover, without considering species-specific differences or functional traits (Gardner et al. 2003, De'Ath et al. 2012). However, corals exhibit a variety of life-history strategies that are reflected in a large range of growth rates and morphologies (Richardson et al. 2017, Zawada et al. 2019a). The identity of the species and their associated traits therefore largely define ecosystem functions and dynamics in coral reefs (Alvarez-Filip et al. 2011, Denis et al. 2017, Zawada et al. 2019b, González-Barrios et al. 2021). There are many coral traits that can be used to estimate functional diversity (McWilliam et al. 2018), but only a small subset contributes to the physical functionality of reefs and controls its capacity to create complex three-dimensional structures by means of calcium carbonate precipitation (González-Barrios and Álvarez-Filip 2018, Perry and Alvarez-Filip 2019). The three fundamental properties of coral species derived from their functional traits that contribute to reef physical functionality are: coral abundance or cover, calcification rate and structural complexity (González-Barrios and Álvarez-Filip 2018, González-Barrios et al. 2021). From an ecological

perspective, the abundance or cover of individual species dictates their relative contribution in terms of functional traits to the ecosystem. The calcification rate denotes the capacity for reef accretion and regeneration, and how it influences the carbonate budget (Todd 2008, Perry et al. 2012). The structural complexity determines colony morphology and framework character that controls habitat complexity (Gratwicke and Speight 2005, Alvarez-Filip et al. 2011).

Coral populations are declining worldwide as a result of anthropogenic activities such as land-based pollution, overfishing, coastal development and climate change (Hughes et al. 2003, 2017). The resulting widespread coral mortality and the reduction of live coral cover is mediated by organism vulnerability and, as a consequence, human activities have caused non-random changes in community structure and in some cases novel assemblages (McKinney 1997, Bellwood et al. 2004, Alvarez-Filip et al. 2013, Spalding and Brown 2015, Toth et al. 2019). In the western Atlantic, *Acropora* spp. and *Orbicella* spp., both considered important reef-building corals (Jackson 1992, Roff et al. 2020), have been severely reduced and replaced by non-framework building or 'weedy' corals such as *Porites astreoides* and *Agaricia agaricites* (Bruckner and Bruckner 2006, Edmunds and Elahi 2007, Green et al. 2008, Rodríguez-Martínez et al. 2014, Perry et al. 2015, Estrada-Saldívar et al. 2019). However, the characteristics of these 'weedy' species prevent them from fulfilling the functional role of the former reef-building species (González-Barrios et al. 2021), therefore, compromising key ecosystem functions and services (Perry et al. 2018, Estrada-Saldívar et al. 2019, Perry and Alvarez-Filip 2019).

Understanding how such novel ecological assemblages have diverged from pre-disturbance or pristine ecological states is fundamental to predict the implications of these changes for ecosystem functioning and services (Schwerdtner Máñez et al. 2014, Thurstan et al. 2015). For that it is crucial to know the initial or baseline state of the community prior to human-induced changes or at a particular point in history (Kopf et al. 2015, Nogué et al. 2017). Such ecological baselines not only help quantify the extent of community change but also can help guide more effective conservation and management (Pitcher 2005, Schwerdtner Máñez et al. 2014).

Determining ecosystem baselines is challenging owing to the absence of reliable historical data (Bruno et al. 2014, Eddy et al. 2018). Very little is known about natural states of coral reefs, and most of historical data are usually defined at regional scale for a few reef locations and with a high level of uncertainty and potential biases (Knowlton and Jackson 2008, Eddy et al. 2018, Meesters et al. 2020). Moreover, attempts to estimate the pre-human baseline condition do not always consider species habitat preferences or large-scale environmental influences, which have a fundamental effect on the natural states of ecosystems (Bruno et al. 2014, Stein et al. 2014, McGarigal et al. 2016). In the absence of reliable historical data, a promising approach is therefore to reconstruct these baselines from ecological models of past ecosystems. Such approaches have been used to model historical changes in marine food webs or to construct models for

past ecosystems to design sustainable fisheries (Pitcher 2005, Lotze et al. 2011).

Ecological niche models (ENM) have been widely used to study the ecological requirements of species by relating their known distribution to a set of relevant environmental variables (Peterson 2006), often focusing on species as individual entities. In recent years, however, new approaches have attempted to model different structural or compositional aspects of the assemblage (Pottier et al. 2013, D'Amen et al. 2017, Grenié et al. 2020). Such is the case of the so-called stacked species distribution models, which starts from modeling individual species to later stacking them to form assemblages (Dubuis et al. 2011, Guisan and Rahbek 2011).

Species richness is often the main property of the assemblages estimated using stacking models, and functional traits are often used to constrain species distributions or as assembly rules to reduce species richness overprediction (Guisan and Rahbek 2011, D'Amen et al. 2015). However, coupling the functional traits of habitat-forming species to the niche models estimating species fundamental niches, can also enable an estimate of the potential of physical functionality of communities across extensive areas, which we refer to as reef functional potential. This niche-trait based approach may therefore provide a promising way to link species environmental preferences, environmental variability and functional traits to improve inferences on the impact of environmental change on biodiversity and ecosystem functioning (Kearney et al. 2010, Funk et al. 2017).

To spatially estimate the reef functional potential (RFP) of Greater Caribbean coral reefs, we integrate ecological niche models of 49 reef-building coral species with morpho-functional traits. The modeled results are then compared to current estimates of the reef physical functionality derived from field data to quantify the degree of divergence of reefs along the western Caribbean. Our approach predicts the capacity to create complex three-dimensional structures rather than only portraying potential species distribution ranges. Because we use only environmental predictors, the estimates of reef functional potential do not consider other natural or anthropogenic disturbances acting over these ecosystems. Similarly, species richness and the functional characteristics of the communities are assumed to be controlled by the environment without consideration of processes such as biotic interactions and dispersal that shape ecological assemblages (D'Amen et al. 2017).

Methods

Species occurrence records

To create a geodatabase of occurrence records of Atlantic shallow-water reef-building corals we conducted a systematic search using the following sources: The Global Biodiversity Information Facilities (<www.gbif.org/>, GBIF Occurrence Download <<https://doi.org/10.15468/dl.iwb5jx>> (4 Sept 2017), GBIF Occurrence Download

<<https://doi.org/10.15468/dl.n9x4nb>> (12 Feb 2019)), the Ocean Biogeographic Information System (Ocean Biodiversity Information System (OBIS), Intergovernmental Oceanographic Commission of UNESCO, <<https://obis.org/>>), Biodiversity Information Serving Our Nation ((BISON), accessed 12 Feb 2019, <<https://bison.usgs.gov/#home>>), the Time Series Coral-cover from Florida and the Virgin Islands (Guest et al. 2018), the Caribbean Coastal Marine Productivity Program database (Linton 2001), the Atlantic and Gulf Rapid Reef Assessment database (Marks and Lang 2018), and data from the laboratory of Biodiversity and Reef Conservation, which was curated, systemized, and is now included in the Caribbean Reefs Information System database. Additionally, we performed a literature search to incorporate occurrence data for reef areas that appeared to be underrepresented when the pooled occurrences were plotted in the geographic space (i.e. none or very few records). Those areas were in Cabo Verde, Cuba, Guatemala, Honduras, Mexico, Nicaragua, Puerto Rico, Dominican Republic and Flower Garden Banks in USA (Supporting information). The compiled occurrences were reviewed to exclude duplicated coordinates per species, data coming from the fossil record and data with georeferencing errors (i.e. records on land).

Dataset treatment

Two important assumptions when developing niche models are that species are in equilibrium with the environment within their native range, and that the species niches are conserved over time (Richmond et al. 2010). The violation of these assumptions can cause underprediction of potential areas of suitability. In the case of Caribbean corals, there is evidence supporting that species composition and distribution ranges have been nearly homogeneous, even at geological time scales (Jackson 1992, Miloslavich et al. 2010, Veron et al. 2015). For instance, Toth et al. (2019) demonstrated that species composition in the Florida Keys Reef Trak has remained relatively stable since the Holocene. Yet, to avoid the violation of these assumptions in our models, we used short-time scale occurrence data for model calibration (from 1950 to 2019).

One more consideration regarding occurrence data is the effect of sampling bias on model performance. Most algorithms estimate the species environmental requirements by correlating occurrence records with environmental variables (Warren and Seifert 2011), which makes them especially sensitive to sampling bias and spatial autocorrelation (Segurado et al. 2006, Phillips et al. 2009). Geographical biases in occurrence data often result in environmental biases, which may lead to inaccurate models (Phillips et al. 2009, Yackulic et al. 2013). Despite the recognition of the importance of sample bias on ecological niche models, currently, there is no consensus about how to properly address this problem. To cope with this, we applied a spatial filter with a minimum nearest-neighbor distance between points in order to reduce spatial clumping of occurrences (Veloz 2009, Kramer-Schadt et al. 2013, Boria et al. 2014). To select

the proper distance for the spatial thinning of occurrence data we tested models using ten coral species with different sample sizes and geographic range sizes as test examples. One group of models had no spatial thinning of the occurrence data; this yielded strong model overfitting coincident with a higher density of occurrences. A second group of models was run with a spatial filtering of 20 km applied to all data, and a third group was run with occurrences split in subsets according to different geographical clumping, where the data corresponding to the western Caribbean basin (higher clumping) was filtered with a distance of 40 km, and the rest of the data with a distance of 20 km. The resulting model outputs were converted to presence–absence maps using the minimum training presence threshold to cut off habitat suitability (Kramer-Schadt et al. 2013). We visually compared the two sets of presence–absence models with filtered occurrences against those generated with no thinning. As a result, we decided to use the 40–20 km filtering as these models showed a reduction in model overfitting, and better represented the known distribution of species. Once occurrence data were spatially filtered, the resulting subset was used as the training dataset, and the occurrences not included were used as testing dataset.

Spatial autocorrelation (SAC) is known to be an issue in distribution models. We investigated SAC in the data sets before and after the filtering process using the Moran's I statistics (R package 'ape' V 5.5, Paradis and Schliep 2019), and observed a substantial reduction in the SAC after the filtering process (Supporting information). We decided not to eliminate the remaining SAC further as we would risk underestimating the importance of the variables and losing explanatory power (Araújo and Williams 2000, Sillero and Barbosa 2021). Moreover, given that many abiotic factors commonly used in species distribution models are only independent at very long distances (Levin 1992), the control of SAC at large spatial scales is usually necessary when environmental factors are not considered the main drivers of ecological patterns (Diniz-Filho et al. 2003). Thus, we assumed that the remaining SAC in our data did not represent a problem as the models were calibrated at a macro-scale and were based on environmental controls.

Species selection

To select the species to be modeled, we applied a filter for those with more than 15 occurrence records after data treatment, resulting in a total of 49 coral species. The selected species represent approximately 48% of corals (scleractinia and hydrozoa) reported for the Caribbean ($n=102$, Miloslavich et al. 2010) and include the main reef-builders in the region (Jackson 1992). These species exhibit different life-history strategies classified as competitive, 'weedy', stress-tolerant and generalists based on a trait-based approach accounting for colony morphology, growth, calcification, reproductive mode and symbiont richness (Darling et al. 2012). Furthermore, the species display different distributional ranges such as *Dendrogyra cylindrus*, constrained to the

Caribbean basin, *Acropora cervicornis* and *A. palmata* which are found in the Caribbean and Gulf of Mexico, and species such as *Porites astreoides* and *Siderastrea siderea* which are also found in reefs from Brazil and among coral communities in west Africa.

Calibration areas

Choosing the extent of the calibration area (M) for ecological niche modelling is a key step to produce accurate models, preferably defined as the geographic region that has been accessible to the species over relevant time periods and reflects its ecology and evolutionary history (Barve et al. 2011). In the case of marine organisms, delineating the calibration area represents a challenge because of the lack of physical barriers and the fact that, for most organisms, dispersal depends upon ocean currents (Melo-Merino et al. 2020). Corals have complex life histories, including a larval phase that allow a greater dispersal through ocean currents, but whose success depends largely on the characteristics of the larvae (e.g. lifespan, presence of symbionts) and on environmental conditions, so they may not be able to occupy all areas to which they have access. Although the area of interest in this work is the Greater Caribbean, we considered it important to include the entire distribution of the species to make the niche estimation as realistic as possible. Therefore, we decided to use all the regions occupied by the species to calibrate the models. As a result, we defined two calibration areas dividing coral species into those that inhabit the Caribbean and Gulf of Mexico (M Greater Caribbean), and those that occupy a wider extent in the Atlantic and are found in Brazilian reefs and coral communities in Africa (M Atlantic; Supporting information).

Environmental predictors

We selected the environmental predictors recognized to influence the distribution of reef corals (Kleypas et al. 1999), and that have been used in other niche and distribution models for shallow water corals performed on a global scale (Couce et al. 2012, Freeman et al. 2013). These environmental variables are temperature, current velocity, diffuse attenuation coefficient, dissolved oxygen, nitrate, photosynthetically available radiation (PAR), phosphate, salinity and omega aragonite. We used the minimum, mean and maximum for each variable (but omega aragonite) from the Bio-ORACLE climate dataset (Tyberghein et al. 2012, Assis et al. 2018), except for PAR for which only the maximum and minimum were available and for pH for which only the mean was available. Additionally, we calculated the mean omega aragonite through the CO2calc software designed to estimate carbonate system parameters (Robbins et al. 2010) using salinity, temperature, total alkalinity (calculated following Lee et al. 2006), pH and depth (as proxy of pressure) as input values. All environmental predictors were downloaded and/or calculated at a 5 arcmin (~9 km) spatial resolution, and for the ocean surface layer.

The final set of environmental predictors used to calibrate the models was selected using a combined procedure. We estimated the correlation among all metrics by Pearson's correlation coefficient and explored their contribution via a jack-knife procedure implemented in preliminary Maxent models. For each species, the predictors with the highest contributions were usually derived from the same variable (e.g. dissolved oxygen max, min and mean, followed by diffuse attenuation max, min, and, mean) that showed strong correlations with each other. We therefore decided to perform an initial selection of predictors among groups of variables. We started by comparing the first two groups with the highest contributions and chose the metrics with the highest contributions if they were not correlated with each other. In the case where the metric with the highest contribution in one group was highly correlated ($r > 0.85$) with the highest in the second group, the one with the largest contribution was preferred over the other, and in the second group, the selected metric was the one uncorrelated with those previously selected. In the case of omega aragonite and pH that only had mean values and were correlated with each other, we selected the one with the highest contribution. We decided to use a single set of environmental variables for all the species since it is expected that closely related species occupy similar environmental niches (Wiens et al. 2010). For the final selection, we considered the variables that appeared with more frequency as the most important (estimated as percentage of relative contribution). The final selection included nine variables: minimum current velocity, minimum diffuse attenuation, minimum dissolved oxygen, maximum nitrate concentration, maximum PAR, mean pH, maximum phosphate concentration, minimum salinity and mean temperature (Supporting information).

Ecological niche models calibration and evaluation

We used the presence-background algorithm of Maxent ver. 3.4.1 (Phillips et al. 2006) as implemented in the 'kuenm' package (Cobos et al. 2019) in the R statistical environment (<www.r-project.org>). This package provides an automated way to tune the models by testing all possible combinations between regularization multipliers, feature classes and environmental predictors to choose the combination that best explains the data provided. We explored different parameterizations using 493 candidate models generated through the interaction of 17 regularization multipliers (from 0.1 to 1 with intervals of 0.1, 1.5, 2, 2.5, and from 3 to 6 with intervals of 1), and all 29 possible combinations among five feature classes (l=linear, q=quadratic, p=product, t=threshold and h=hinge). The selection of the best candidate models was based on model significance, predictive ability and model complexity as implemented in 'kuenm'. First, the models were selected based on statistical significance using a partial ROC analysis (partial receiver operating characteristic; Peterson et al. 2008). Second, statistically significant models were tested to omission criteria using a threshold of 10% training omission rate ($E = 10\%$; Muscarella et al. 2014). Finally, model complexity was evaluated through the Akaike

information criteria corrected for small sample sizes and the models with the lowest AICc values were selected (Warren and Seifert 2011, Muscarella et al. 2014). With this framework for model selection (statistical significance, low OR and low AICc) the best models for the individual species showed different model parameterizations, but all models showed a good performance (Supporting information).

Final models for each of the 49 coral species were created using the specific settings from the best model and calibrated in their corresponding M (Greater Caribbean or Atlantic; Supporting information). We generated ten replicates of the model by bootstrap resampling for each species using the training-data subset. We selected the logistic output format, which estimates environmental suitability represented in a continuous scale from 0 (not suitable) to 1 (most suitable). To represent habitat suitability, we used the median values across replicates. When more than one model was selected as the best, we calculated the median among all models.

To evaluate final model performance, we used the AUC ratio and statistical significance of the partial ROC (area under the curve of the receiving-operating characteristic; Peterson et al. 2008). This metric takes values from 0 to 2 where values greater than 1 indicate that the predictions of the model are better than random. For all the models we allowed an omission rate of 10% ($E = 10\%$) and evaluated statistical significance of the partial ROC analysis. For all the species, models showed a good performance, with AUC ratios greater than 1, and all being statistically significant (Supporting information).

Coral reefs functional potential estimation

To estimate the reef functional potential (RFP) of Greater Caribbean reefs, we created a functionality metric by combining environmental suitability obtained using the Maxent models with coral morpho-functional traits.

We chose traits that are fundamental for determining the physical functionality of coral species in reef environments: calcification rate and skeletal complexity (given by colony rugosity and height). These morpho-functional traits are assumed to be strongly related with the functional role of corals in the ecosystem (González-Barrios and Álvarez-Filip 2018). Moreover, coral morphology has been considered to be an important part of a coral 'super trait' that captures large variations of biological and ecological processes (Madin et al. 2016). For the inclusion of coral morpho-functional traits, we used a previously published calculation of Caribbean coral species functional coefficients related to their capacity to build complex three-dimensional structures estimated by González-Barrios and Álvarez-Filip (2018). They used a combination of published literature and field data on extension rate, skeletal density and morphometric data to estimate corals calcification rates ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) and colony complexity represented by its rugosity and height. Those three metrics were first standardized, and then averaged to represent the functional coefficient (FC) of the species, denoting their capacity to create complex three-dimensional structures in a reef. For those species not included in their publication

(six species), we estimated their functional coefficient following González-Barrios and Álvarez-Filip (2018) methodology.

The Maxent output can be considered as a measure of environmental suitability, where higher values represent optimal conditions for the species (Phillips et al. 2006). So, as a first step before the stacking process we performed a raster operation to multiply the suitability raster layer of each species by its functional coefficient. Having done this, we estimated the RFP by stacking the product rasters based on the sum of the 49 raster layers derived from the multiplication (Fig. 1).

RFP layer post-processing

To restrict the area of analysis to the areas with reef development, the final output representing the RFP was cropped

using a reef layer. To create this layer, we used the global map of shallow tropical coral reefs created by the World Resources Institute for the Reefs at Risk Revisited project (Burke et al. 2011). First, we created a fishnet shapefile with the same spatial resolution as the environmental variables (5 arcmin) encompassing the extent of the Greater Caribbean. Then, we selected all the cells in the fishnet that intersected with the reefs polygons. We added some additional reef locations that were absent in the initial polygon layer, located in the southwest Gulf of Mexico, the north of San Andres Archipelago, Honduras, Guatemala, Bahamas and Flower Garden Banks (Supporting information).

Once the RFP was limited to the areas with reef development, we analyzed the spatial patterns of the RFP using the ecoregion classification of the Marine Ecoregions of the

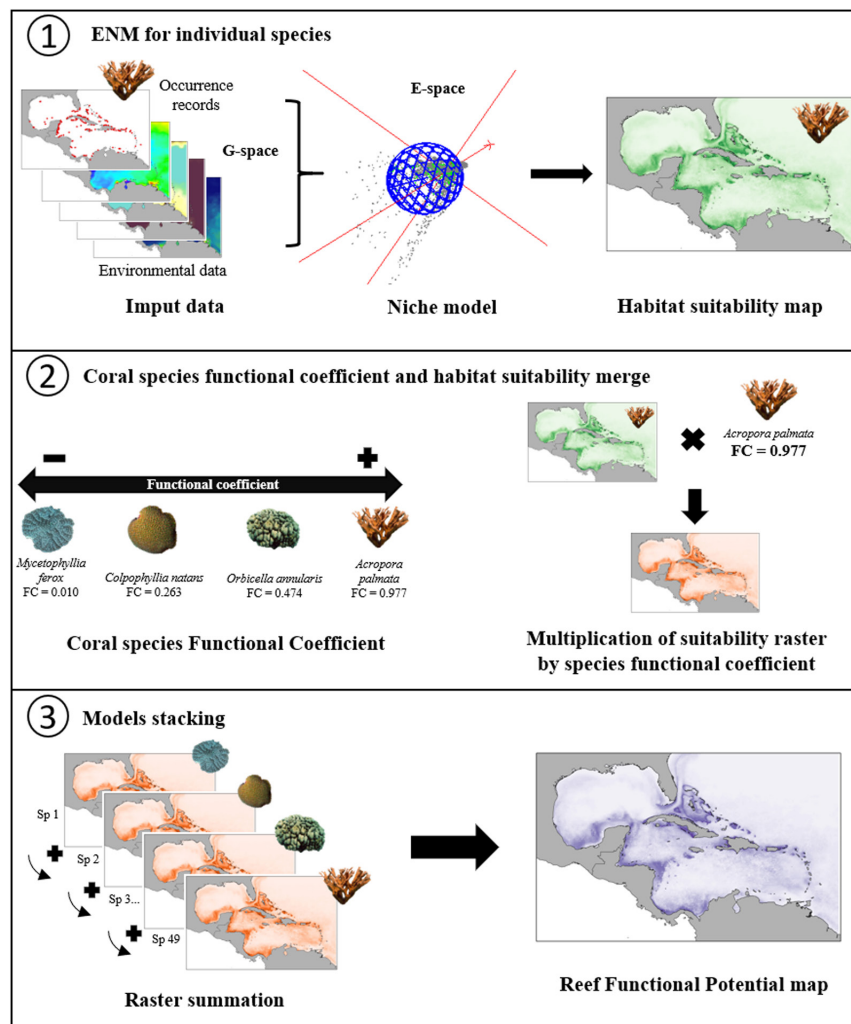


Figure 1. Schematic representation of the reef functional potential estimation procedure. Step 1: Generation of individual ecological niche models for the 49 species. Here, species occurrence records and environmental variables are interpreted by the algorithm in the ecological space, and then projected again in the geographic space as a suitability map. Step 2: Coral species functional coefficient and habitat suitability combination. Example of species with low, medium and high functional coefficient. Here, the habitat suitability raster is multiplied by the species functional coefficients. Step 3: Summation of the 49 raster layers obtained through the multiplication procedure to calculate the reef functional potential.

World (Spalding et al. 2007). To determine the differences in the mean RFP among ecoregions we performed a one-way ANOVA test and a pairwise post hoc comparison Tukey test.

Hotspot analysis

To identify zones with the highest RFP we used the Getis-Ord G_i^* hotspot analysis (Getis and Ord 1992). This method compares proportionally the local sum of the variable (RFP value) in each cell and its neighbors with all the cells in the study area to measure the intensity of clustering of high or low values. When the local sum is higher or lower than expected by chance, the G_i^* has large positive or negative values. Thus, a z-score is estimated for each cell, where a large positive z-score denotes a hotspot and a large negative z-score a coldspot. As a z-score derived from a standard normal distribution, no further calculations are required. We conducted the Getis-Ord analysis with the function available in the ArcGIS 10.5 environment (Environmental Systems Research Institute (ESRI) 2015, ArcGIS desktop ver. 10.3).

Divergence of coral reefs functional potential

To estimate the degree of divergence in the RFP we used the western Caribbean (also known as the Mesoamerican reef) as study case. This region has been extensively surveyed to monitor coral reef condition along the ~1000 km reef system located within Mexico, Belize, Guatemala and Honduras, which is composed of fringing reefs, barrier reefs and atolls (Gress et al. 2019). For this analysis we used published information on the estimation of the reef functional index (RFI; González-Barrios and Álvarez-Filip 2018), complemented with information obtained through the Caribbean Reefs Information System database. Data collection follows the AGRRA protocol point intercept (Lang et al. 2010) and ReefBudget (Perry et al. 2012) methodologies.

A total of 242 sites were included in this analysis covering a period from 2010 to 2017. We selected this period as the coral cover remained relatively stable throughout the region given the absence of severe disturbance events (McField et al. 2018, Contreras-Silva et al. 2020). This period is so representative of the (poor) condition of many reef areas through the Caribbean (Jackson et al. 2014). Before this period, coral cover underwent considerable declines related to thermal anomalies, hurricane impacts, coral diseases and coastal development (García-Salgado et al. 2008, Eakin et al. 2010, Contreras-Silva et al. 2020), but since mid-2000s slightly (~ 5%) recovered, although with no evident effects on reef functionality (McField et al. 2018, Elías Ilosvay et al. 2020, González-Barrios et al. 2021). In 2018 a new deadly coral disease impacted the region, triggering further coral losses (Estrada-Saldívar et al. 2021). When information was available for more than one year for the same site only the most recent was used.

The RFI estimate is based on the species-specific functional coefficient that denotes its capacity to create complex three-dimensional structures and species-level coral cover

data determining the relative contribution of each species to the overall RFI (González-Barrios and Álvarez-Filip 2018). Following Eq. 1, where Lcc_i is the percentage of live coral cover and Fc_i the functional coefficient of the species i .

$$RFI = \sum \left(\frac{Lcc_i}{100} \right) Fc_i \quad (1)$$

The RFI is obtained using the sum of the product of the FC by the cover of each species present in a site. To facilitate the numerical interpretation, the RFI is fourth-root transformed, such that the index varies from almost zero in reefs with low functionality to one in reefs with high functionality (González-Barrios and Álvarez-Filip 2018, Cabral-Tena et al. 2020).

The RFI obtained from field data was plotted against the modeled RFP to which we added an equivalence line. To construct this line, we used 0 as the minimum value for both axes and as maximum, the highest value that could potentially be achieved in each case. In the case of the FRI, the highest value would correspond to a hypothetical site with 100% of coral cover of the species with the highest functional coefficient, corresponding to a RFI of 0.977. In the case of modeled RFP the highest value would correspond to a cell in which the suitability value was 1 for all the 49 modelled species, in this case the RFP would be of 10.568. On the plot, a site with a coherent RFI and RFP values would be close to the line, sites with a higher RFI than RFP would be above the line, and sites with lower RFI than RFP would be below the line. As a measure of divergence from the RFP, we used the distance of each point to the equivalence line that we further transformed into percentage values.

Results

Reef functional potential

In general, distribution models for the 49 coral species showed a good representation of the known present-day species distributions. Using the stacked models, we found that Greater Caribbean marine ecoregions presented a high degree of spatial variability in RFP, with values ranging from 0.08 (low) to 9.35 (high) across the entire reef area. The ecoregion with the highest mean value of RFP was the western Caribbean, followed by the Floridean, Bahamian, Greater Antilles and the southwestern Caribbean (Fig. 2a). In contrast, ecoregions with the lowest RFP were Bermuda and the northern Gulf of Mexico (Fig. 2a). The western Caribbean was the ecoregion with the highest number of cells with high RFP values. Conversely, the southern Caribbean showed low values of RFP except for the Morrocoy National Park, Los Roques and Isla las Aves in Venezuela. The one-way ANOVA confirmed significant differences between ecoregions ($p < 0.05$). The pairwise-comparison test showed differences especially for the western Caribbean, which was significantly different to all other ecoregions (Fig. 3). The hotspot analysis identified the highest RFP along the coast of Belize and the

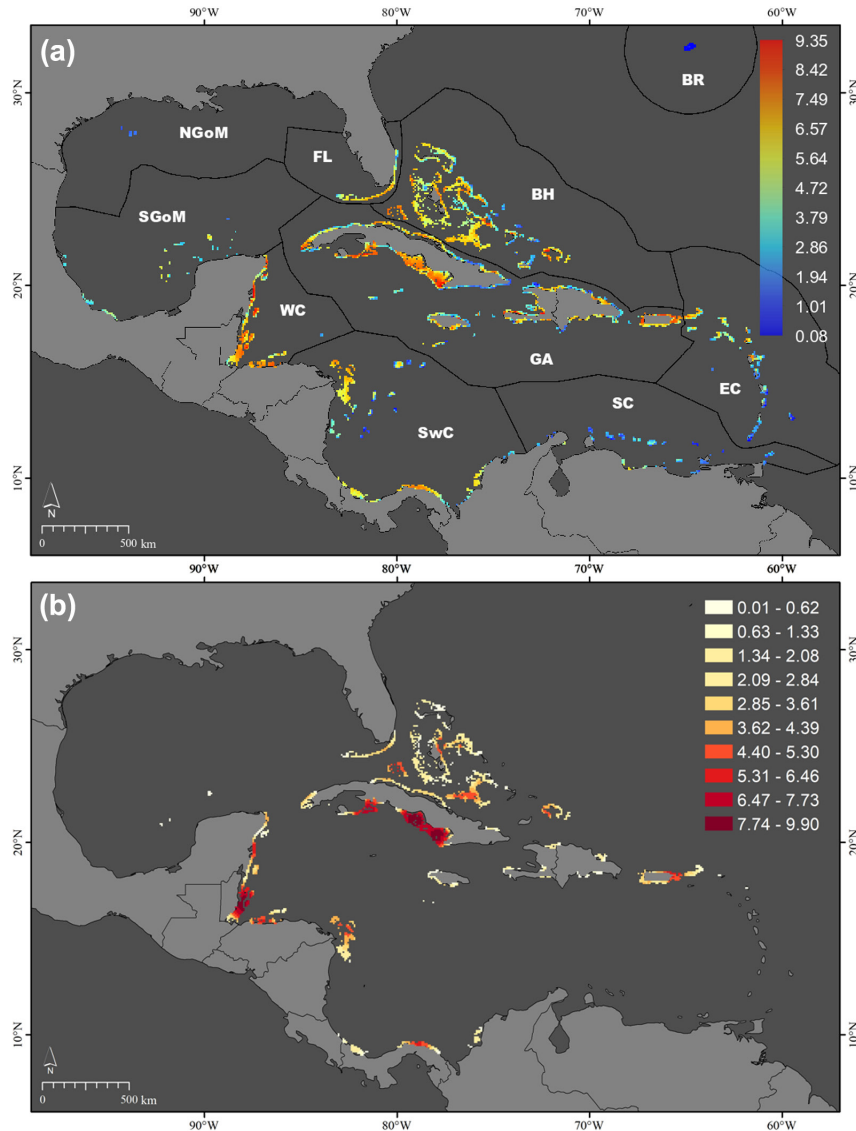


Figure 2. Reef functional potential (RFP) and hotspot analysis of Greater Caribbean coral reefs. (a) Distribution of the RFP among ecoregions represented by the black lines: NGoM: northern Gulf of Mexico, FL: Floridian, BH: Bahamian, BR: Bermuda, SGoM: southern Gulf of Mexico, WC: western Caribbean, GA: Greater Antilles, EC: eastern Caribbean, SwC: southwestern Caribbean and SC: southern Caribbean. (b) Hotspots of reef functional potential in the Greater Caribbean using the Getis-Ord hotspot analysis. Legend shows the Getis-Ord G_i^* z-score values.

southeast coast of Cuba, followed by the central coast of the Yucatán Peninsula in Mexico, the west coast of Honduras, Cay Sal Bank in the Bahamas, the eastern Puerto Rico and the Kuna Yala province of Panama (Fig. 2b).

Divergence in reef functional potential

Of the reefs in the western Caribbean, 84% showed a reduction in their physical functionality with respect to the RFP estimation (blue dots; Fig. 4a), and nearly half of the sites presented a reduction superior to 30% (dark blue dots; Fig. 4a). Conversely, only a small proportion of sites, mainly located in Roatan island, Honduras and the north and south of the Mexican Yucatan peninsula showed higher RFI values than

those expected by the models, and the majority with a low difference ($< 15\%$; red dots; Fig. 4a). We observed a spatially consistent pattern of decrease in physical functionality of reefs along the western Caribbean. Sites with the most drastic losses are mainly located in the north of the Yucatan peninsula and the Sian Ka'an Biosphere Reserve in Mexico, central and southern Belize and coastal Honduras (Fig. 4b). On average, the physical functionality of the western Caribbean reefs has decreased from the expected values by 30% ($\pm 15\%$ SD). Some of the reefs with the highest levels of decrease in physical functionality are located inside hotspot zones. A Spearman correlation analysis between percentage of divergence and hotspot G_i^* Zscore value showed a low but significant negative correlation ($p < 0.001$, $\rho = -0.47$; Fig. 5).

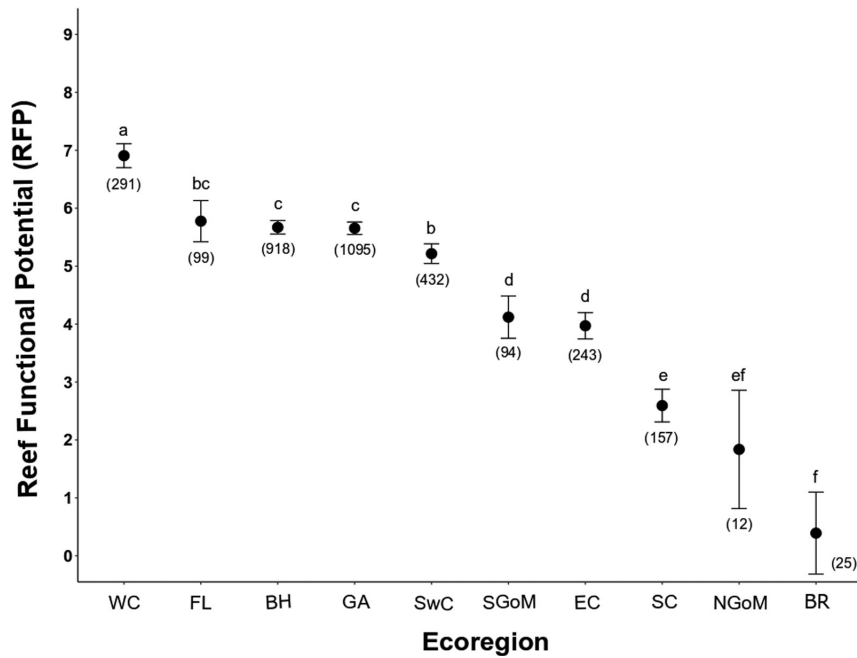


Figure 3. Mean reef functional potential per marine ecoregion. Error bars represent the confidence intervals at 95%. Letters above the bars denote levels of significance, the means that do not share a letter have a difference that is statistically significant. Numbers in parentheses denote the n or number of cells in each ecoregion.

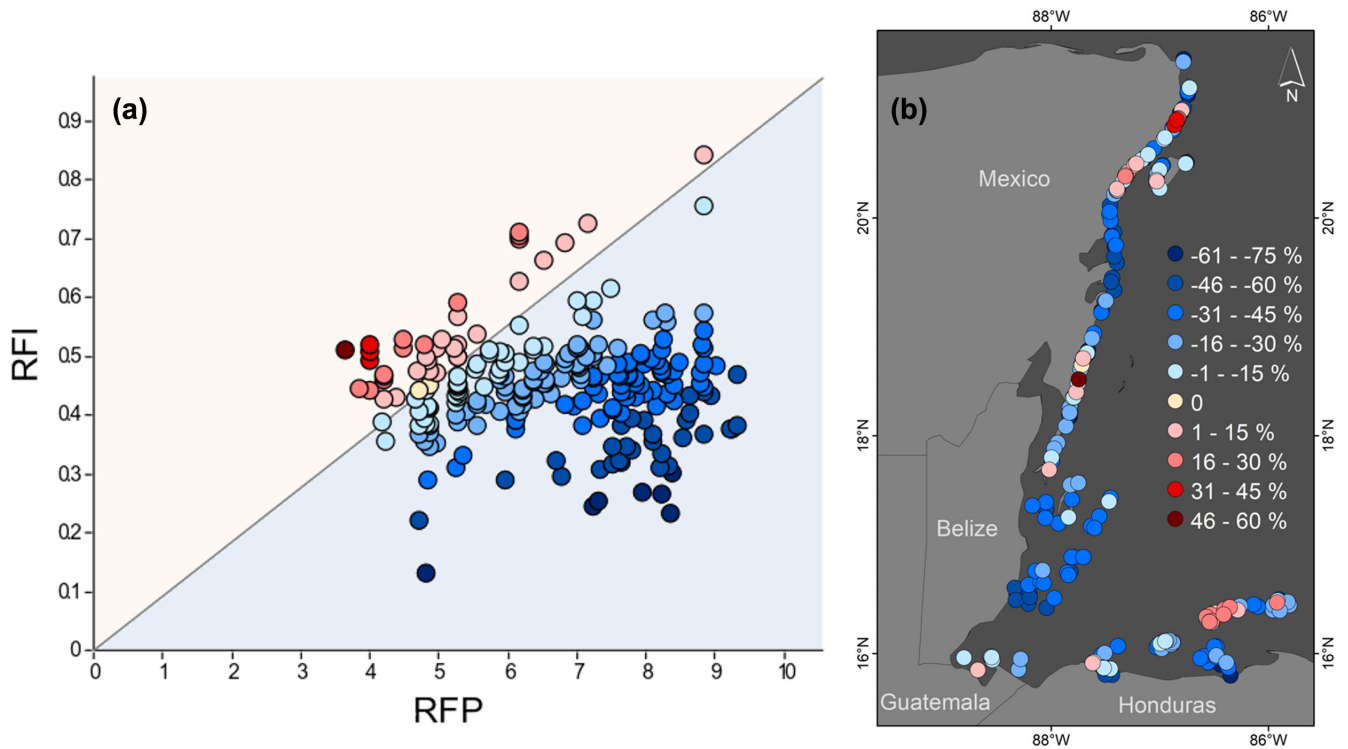


Figure 4. Divergence of reef functional potential. (a) Comparison between reef functional index (RFI) estimated with field data and reef functional potential (RFP) estimated through the models. Black line represents the correspondence between observed and predicted reef functioning. Red points above the regression line correspond to sites with observed values higher than modeled values. Blue points below the line correspond to sites with lower observed values than modeled values. The distance from the line represents a measure of the divergence from reef functional potential. (b) Representation of the divergence from reef functional potential in the geographic space, where legend represent values expressed as percentage.

Discussion

In this study, we show that the combination of ecological niche models and species morpho-functional trait metrics is a promising approach to estimate the large-scale functional potential of ecological communities in the absence of anthropogenic disturbance. This approach directly incorporates a measure of the species performance and accounts for environmental variability, species environmental preferences and species-specific morpho-functional traits. Our findings reveal a highly variable reef functional potential (RFP) among reef areas within the Greater Caribbean ecoregions, but with lower values, as expected, in marginal environments. Furthermore, for the great majority of reefs in the western Caribbean, the potential for physical functionality has decreased by ~30% when compared with the RFI. These findings have important implications in evaluating the degree of degradation of coral reefs, as well as for the management, conservation and restoration of reef ecosystems.

The high degree of variation in RFP across ecoregions suggests a strong effect of local environmental conditions for reef development. Spatially adjacent coral reef areas can exhibit high environmental variability, which is reflected by different community structure, which in turns results in functional variation across assemblages (Alvarez-Filip et al. 2013, Gove et al. 2015, Zinke et al. 2018). The Caribbean basin exhibits a spatially heterogeneous physicochemical environment, mainly induced by local-scale variability in river outflow, terrestrial runoff, upwellings and bathymetric effects (Chollett et al. 2012). In our study, areas characterized by low values of RFP were located at the limit of reef development. At higher latitudes, environmental parameters such as temperature, light availability and aragonite saturation draw environmental limits for coral growth and reef development and, in some cases lead to a reduced coral diversity associated

with the marginality of environments (Kleypas et al. 1999, Perry and Larcombe 2003). Likewise, we observed low values of RFP in the southern Caribbean ecoregion. This portion of the Caribbean is subject to the influence of the southern Caribbean upwelling system that causes seasonal variability in light intensity, water temperature, salinity and nutrient concentrations, which invariably modifies abiotic conditions under which reefs develop (Rueda-Roa and Muller-Karger 2013, Eidens et al. 2014). For this reason, the southern Caribbean ecoregion exhibits different environmental conditions than the rest of the Caribbean basin, which caused the Maxent algorithm to identify it as less optimal for reef development. This is consistent with what has been described for reefs along the coast of Venezuela, where, in addition to the effect of the upwelling system, river outflow and unstable substrate (i.e. sandy bottoms) prevent a good reef development, leading to small coral communities with low diversity and no accretion, especially in the eastern portion (Weil 2003). However, our models accurately identified the areas where important reef development occur in the mainland of Venezuela located in the Morrocoy and San Esteban national Parks, and in the offshore islands in Los Roques Archipelago and Isla las Aves (Weil 2003, Debrot et al. 2019).

Areas characterized by high RFP were found particularly in the western Caribbean, which has been recognized as a biodiversity hotspot and considered as a conservation priority with great ecological and economic value (Olson and Dinerstein 2002, Roberts et al. 2002). The high values of RFP observed in this ecoregion might be explained by the attributes of the reef system and the seascape. In the western Caribbean is located one of the largest reef formations in the Caribbean constituted by a near-continuous reef system of about 1000 km long (Gress et al. 2019). This particularity confers a spatial continuity of the habitat favoring the connectivity between biological communities. As in terrestrial ecosystems,

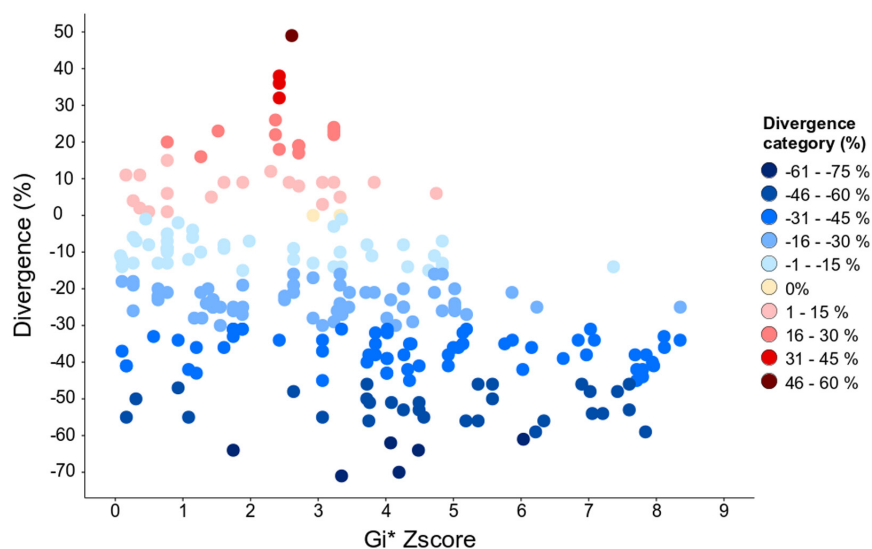


Figure 5. Relationship between the divergence from reef functional potential and hotspot value estimated using the G_i^* Zscore. The graph shows a low but significant negative correlation among variables (Spearman's $\rho = -0.47$, $p < 0.001$).

forests with a long temporal and near-continuous presence are often associated with high biodiversity (Mölder et al. 2019). Another attribute of the western Caribbean reef system that allows it to support a high diversity is the area available for species. The species–area relationship suggests that larger areas support higher richness (Lomolino 2001). This has been observed in coral reefs where species richness and density of coral colonies increase in larger reefs (Huntington and Lirman 2012).

The observed reduction in the physical functionality of reefs in the western Caribbean is consistent with their historical degradation. Live coral cover across the Caribbean basin has declined drastically in recent decades, with reductions of up to ~80% (Gardner et al. 2003, Côté et al. 2005, Contreras-Silva et al. 2020). These declines, however, have not been consistent across functional groups of reef building corals (Bruckner and Bruckner 2006, Edmunds and Elahi 2007, Rodríguez-Martínez et al. 2014). For instance, the mass mortality of *Acropora palmata* and *A. cervicornis* due to local human impacts and disease outbreaks killed ~80% of their populations (Gladfelter 1982, Cramer et al. 2020). This mass mortality of reef-building *Acropora* spp. has heavily altered the structure and functioning of Caribbean reefs, due to their fast growing, high carbonate accumulation rates and large branching morphology (Lange and Perry 2019).

Accompanying the demise of key reef-builders, many Caribbean reefs have undergone relative increases in the dominance of non-framework corals which despite providing benefits as carbonate producers and protection from erosion (Perry et al. 2015, Toth et al. 2018), contribute considerably less to the physical functionality of the reefs (González-Barrios and Álvarez-Filip 2018). Furthermore, even though some reefs have experienced a recovery in terms of live coral cover (Edmunds and Carpenter 2001, Contreras-Silva et al. 2020), most of these recoveries concerns non-framework ‘weedy’ corals, particularly *P. astreoides* and *A. agaricites* (Green et al. 2008, Perry et al. 2015). A recent study revealed that despite a low but significant increase in coral cover, the physical functionality of reefs was not considerably improved, owing to the life-history traits of the species that contributed most to the increase (González-Barrios et al. 2021). At present, coral reefs are still under increasing pressures from climate change, diseases, coastal development and the loss of ecosystem resilience (Roff and Mumby 2012, Hughes et al. 2018, Suchley and Alvarez-Filip 2018, Perry and Alvarez-Filip 2019, Estrada-Saldívar et al. 2020), which compromise their physical functionality and could even further exacerbate the reduction in functionality observed in this study.

Despite the considerable loss in physical functionality at most western Caribbean sites, our findings also show that some have a higher RFI than predicted by the models (i.e. RFP). One likely explanation for this counterintuitive increase is the disproportionate weight that single species with high functional contribution provide when they are present in the reefs at a relatively high cover. An obvious example is the genus *Acropora*, as these species consistently have the highest calcification rates and morphological

complexity (González-Barrios and Álvarez-Filip 2018), and when present at relatively high cover (even more than 80% of relative cover) increase the RFI disproportionately. For instance, on the southwest coast of Roatan, Bay Islands, Honduras an extraordinary high cover for *A. cervicornis* has been reported (Keck et al. 2005, Riegl et al. 2009); similarly, in the northeast of the Mexican Caribbean, surveys report some of the most prolific populations of *A. palmata* in the western Caribbean region (Rodríguez-Martínez et al. 2014). Also, at Coral Gardens off the Belize coast, large populations of both species of *Acropora* also occur (Busch et al. 2016, Greer et al. 2020). A similar but lower effect is also identified when other functionally important species occur at high levels of coral cover (e.g. *Orbicella* spp, *Agaricia tenuifolia* and branching *Porites* spp.) (González-Barrios and Álvarez-Filip 2018, González-Barrios et al. 2021).

A more consistent finding is that the greatest losses in functional potential occur at those sites that initially had considerably high functional potential (Fig. 5). Given that anthropogenic impacts are global, the geographic distribution of these effects are not uniform, and the most affected ecosystems are in tropical regions because of their high biodiversity (Dirzo et al. 2014, Young et al. 2016, Barlow et al. 2018). For example, the Brazilian Atlantic forest is a bird-diversity hotspot and has been identified as a priority area for conservation; nevertheless the deforestation is so high that many species have likely been eliminated from their habitat (Jenkins et al. 2013). Similarly, diverse tropical coral reefs are extremely vulnerable to human-related stressors and are often highlighted as ecosystems of conservation priority (Roberts et al. 2002). Coral reef hotspots have been defined following the more traditional hotspot definition proposed by Myers (1988) that considers attributes such as species richness, endemism and threats for their delimitation as a biodiversity region of conservation concern (Roberts et al. 2002, Allen 2008). However, it has been pointed out that for corals and reef fishes centers of species richness and endemism are not spatially concordant with hotspots (Hughes et al. 2002). Furthermore, studies considering other facets of biodiversity, such as functional diversity, argue that establishing conservation strategies should not only be conducted based on species richness patterns (Stuart-Smith et al. 2013, Grenié et al. 2018). In the Caribbean region, the identified RFP hotspots occur where environmental suitability and coral-species configuration enable high calcification capacity and the formation and accumulation of complex three-dimensional frameworks. This functionality approach allows the inclusion of reef structural complexity as an important attribute in the identification of targets for reef conservation or restoration, which would be valuable for maintaining and protecting their functional integrity.

In the absence of historical baselines, our approximation of the physical functional potential of reefs by integrating niche models and morpho-functional traits allows to estimate the large-scale functionality divergence of reefs. This methodology can be transferred to reefs in other geographic regions, as well

as to other species, ecosystems and spatial scales. However, it is important to recognize that coral reefs are highly dynamic ecosystems that can exhibit alternative states of benthic cover composition through time (Norström et al. 2009). Therefore, divergence estimates are dependent on the data used to represent the ‘current condition’ of the coral communities, and results should be interpreted in this context. For example, in this study we used a slice in time (2010–2017) well-known to reflect a degraded state of most Caribbean reefs (Jackson et al. 2014), including our study region (Contreras-Silva et al. 2020).

In addition, we identified possible opportunities for improvement of our approach. First, we assumed that the 49 modelled species are present in all reef areas, and their contribution to the functional potential is proportional to environmental suitability. This ignores evidence of the role of biotic interactions on species distribution patterns and the assembly of ecological communities (Thuiller et al. 2013). Similarly, we did not consider the effects of dispersal capacity, historical and evolutionary processes, and abiotic constraints on the spatio-temporal dynamic of the species ranges and community assembly (D’Amen et al. 2017). Furthermore, factors such as wave energy exposure, hurricanes impact, strong boundary currents, tidal regimens, upwellings and other attributes of the reefs such as geomorphology are known to influence species distributions and diversity patterns on coral reefs (Couce et al. 2012, Veron et al. 2015, Medina-Valmaseda et al. in press). It has also been identified that historical processes such as plate tectonics acting over geological timescales played an important role in defining current tropical reefs biodiversity (Keith et al. 2013, Leprieur et al. 2016). For the Caribbean, major geological events are related to plate tectonics and the closure of the Isthmus of Panama, that separated the Atlantic and eastern Pacific oceans and slowly changed the oceanographic conditions on both sides (Cortés 2007, Reyes-Bonilla and Jordán-Dahlgren 2017). While mechanistic or process-based models that can account for some of the aforementioned factors exist, the nature of correlative models as applied here assumes that species environmental preferences govern their large-scale distribution (Pearson and Dawson 2003), thus, they must be interpreted under this context.

It has also been suggested that to make better spatial prediction of attributes of biological communities, the linkage between species ecological niche and functional traits must be estimated by considering the prevailing environmental conditions at each observation site to capture trait variability along environmental gradients (Guisan et al. 2019). Trait variability can be observed at different organizational levels: within a single individual, among individuals from the same population, and among populations, which implies that trait values are not equally represented across regions (Carmona et al. 2016). One of the causes for intraspecific trait variability is phenotypic plasticity in response to varying environmental conditions (Violle et al. 2012). For corals, it is well acknowledged that their morphology changes in response to prevailing environmental conditions, especially for light irradiance and water movement (Todd 2008). For instance, some foliose species such as the Indo-Pacific coral

Turbinaria mesenterina take a more flattened form under moderate or low light intensity conditions to increase photosynthetic energy acquisition (Hoogenboom et al. 2008). In the tropical Pacific, corals from the genus *Pocillopora* show spatial variation in branch-morphology in response to water flow conditions (Paz-García et al. 2015). Furthermore, the calcification process is affected by environmental conditions: growth parameters such as skeletal density, extension rate and calcification rate can vary for a single species along temperature gradients, and under thermal stress conditions in which calcification rates tend to decrease (Carricart-Ganivet 2004, Carricart-Ganivet et al. 2012). Given that, the performance of coral species can be different within the study area and their functional coefficient may also vary. In our models we did not consider intraspecific trait variability since detailed trait variability is still needed, especially in extensive areas such as the Greater Caribbean. However, we considered that the simplification made using mean trait values is valid to estimate the physical functionality at an ecosystem level, given that the effect of environmental conditions was captured by the niche models, and that interspecific-trait variability should be significantly larger than intraspecific-trait variability (McGill et al. 2006, Carmona et al. 2015). Our functional approach could be strengthened when more detailed morpho-functional trait data, together with a broader taxonomic and biogeographical coverage become available, as in efforts such as the Coral Trait Database (Madin et al. 2016).

In conclusion, our results can provide an important basis for reef protection, management and restoration actions not only based on diversity estimates but considering the ecosystem physical functionality to prevent the loss of key services coral reefs provide. Our approach offers an opportunity to assess how the physical functionality of reefs might change under future climate change scenarios. As environmental changes are expected to continue to occur in coming decades, it is essential to consider how these changes might affect key reef-building corals and the potential consequences on the physical functionality of reef ecosystems. Future studies should focus on the evaluation of habitat suitability changes under different climate scenarios for key reef-building corals, which could in turn help to establish restoration priorities based on habitat suitability from the perspective of species contribution to the physical functionality of coral reefs.

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.0rxwdb27>> (Melo-Merino et al. 2021).

Supporting information

Any supporting information associated with this article is available from the online version.

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