



# Atlantic corals under climate change: modelling distribution shifts to predict richness, phylogenetic structure and trait-diversity changes

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## Abstract

Climate change is altering species distributions worldwide. Particularly, global warming is driving range contractions and expansions of tropical species, such as corals. The use of climatic projections, via species distribution models to predict species distributional shifts, can identify threaten species and help to set priority areas of conservation. In this study, we assessed if distributional shifts of 45 Atlantic reef-forming corals (scleractinian), and the main environmental variables driving their distributions, correlated with their phylogeny and/or their functional traits; i.e. whether expected contractions and expansions affected specific clades, or specific coral traits. We also estimated the potential loss and/or gain of species richness, phylogenetic diversity (PD) and phylogenetic species variability (PSV), as well as the phylogenetic structure of Atlantic reef communities ('clustering', 'overdispersion' or 'randomness'), under a future climate scenario (A2-IPCC-2100). The potential loss of Atlantic corals in the future will be randomly distributed across their phylogeny, i.e. potential extinctions will not only affect one section of the phylogeny, therefore alleviating an inordinate loss of evolutionary history. Nearly all current and future communities presented a 'random' phylogenetic structure. No correlation was found between distributional shifts and coral traits. Environmental variables did not show a significant correlation with the phylogeny neither with coral traits. Predicted changes in species richness, PD and PSV vary across the Atlantic; certain areas display large evolutionary diversity losses. Species belonging to isolated clades (high evolutionary distinctiveness) contribute to quantitative increases, or decreases, of PD and PSV, becoming crucial species for conservation. These findings highlight the importance of combining SDMs with phylogenetic/functional metrics to develop conservation strategies to assess the future of corals.

**Keywords** Climate change · Environmental factors · Scleractinia · SDMs · Phylogenetic diversity · Projections

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## Introduction

Ongoing environmental changes observed in the last decades, such as global temperature rises, glacial retreats, and ocean acidification, are drastically impacting on biotic systems worldwide (Walther et al. 2002; IPCC 2007). In particular, global warming alters organisms' phenology, e.g. plants flower in advanced periods (Menzel et al. 2006). Concurrently, warming temperatures constrains animals' physiology, including reductions in growth and reproduction (Hughes 2000). Warming may also cause high mortality when temperatures exceed organisms' physiological thermal tolerance thresholds (Hughes 2000; Parmesan 2006; García-Robledo et al. 2016). As a result, species distributional shifts are rapidly occurring all over the world (Hampe and Petit 2005; Parmesan 2006; Elith et al. 2010; Chen et al. 2011; Wernberg et al. 2016). For example, some fishes (Cheung et al. 2009; Fodrie et al. 2010; Vergés et al. 2014; Heck et al. 2015) and birds (Wu and Zhang 2015) are expanding their ranges to high latitudes. On the other hand, certain lizards and frogs are being constrained to isolated regions, or even becoming extinct because they cannot reach new areas under favourable environmental conditions (Thomas et al. 2006; Sinervo et al. 2010). Several species, such as certain butterflies, plants and tropical corals are experiencing both situations, i.e. range contractions in their areas of origin, but expanding their range to upper elevations or higher latitudes (Parmesan et al. 1999; Beaumont and Hughes 2002; Precht and Aronson 2004; Wilson et al. 2005; Thomas et al. 2006; Feeley 2012). These shifts can entail biodiversity losses in the areas where species become extent (Díaz et al. 2019); and changes in the settled communities where new alien species compete with the native ones for the habitat, or change the dynamic of the community [e.g. the shift in temperate reef communities of Australia from kelp forests to tropical seaweeds, invertebrates, corals, and fishes (Wernberg et al. 2016)].

Habitat contractions and expansions can be used as an index of species vulnerability to climate change (Guisan and Thuiller 2005; Carvalho et al. 2010); this is also used as a criterion for classifying the conservation status of a species by the IUCN (International Union for Conservation of Nature). These habitat shifts can be predicted by applying Species Distribution Models (SDMs), which estimate the habitat suitability of a species based on the correlation between presence records and environmental gradients (Guisan and Zimmermann 2000). Insight provided by the prediction of species' range shifts (i.e. contraction/expansion) can address diverse phylogenetic questions (Thuiller et al. 2011; Buckley and Kingsolver 2012). For example, the predicted extinction of a species from a community/ assemblage can reduce the taxonomic and the phylogenetic diversity (PD) of such community/assemblage. Aside from richness and taxonomic diversity, measures of PD are widely used to set conservation priorities (Winter et al. 2013; Pollock et al. 2015) with the aim of minimizing the loss of evolutionary diversity (Vane-Wright et al. 1991; Tucker et al. 2017). There is a range of indices to account for different aspects of PD (Tucker et al. 2017); for example, the paramount Faith's (1992) index of PD is defined as the total branch length spanned by the tree, including all species in a local community. This measure depends on the size of the set of species (richness-dependant). However, other metrics of PD are invariant to species richness, such as the  $PD_{SES}$  (standardized effect size) (Webb et al. 2008), or the phylogenetic species variability index (PSV) (Helmus et al. 2007). The  $PD_{SES}$  is used to analyse the phylogenetic structure of a community. When closely related species, belonging to few lineages-clades-taxa, dominate, the community is phylogenetically clustered; the opposite, i.e. a phylogenetically overdispersed community denote a lack of phylogenetic structure. The (PSV) explains how diversity is structured, estimating the

degree of phylogenetic relatedness (or evolutionary redundancy). The amount of PD lost in a community by the disappearance of a species varies depending on its phylogenetic relationships with their community relatives. Importantly, if the losses of species caused by climate change are not randomly distributed across the phylogeny, they can lead to a disproportionate loss of evolutionary history, among other impacts (Nee and May 1997; Heard and Mooers 2000; Thuiller et al. 2011).

The information extracted from SDMs, in terms of the appearance/disappearance of species, along with phylogenetic analyses, can be useful for conservation purposes (Buerki et al. 2015). Thuiller et al. (2011) tested whether certain clades are more vulnerable to climate change than others using mega-phylogenies and predicted geographic changes/range shifts in plants, birds and mammals' suitable areas under different climatic scenarios. They forecasted that the vulnerability of species is weakly clustered across phylogenies, and that future phylogenetic diversity will decrease in southern Europe and increase at higher latitudes and altitudes. Detecting phylogenetic patterns, in particular the prevalence of phylogenetic 'clustering' or 'overdispersion', i.e. whether co-occurring species are more or less closely related than expected by chance, has been widely explored in the scientific literature for decades (Eldredge and Cracraft 1980). If future habitat contractions are connected with phylogenetic 'clustering' across species, i.e., taxonomically similar species share similar values of range contraction, this could represent an important loss of evolutionary history, reflecting the vulnerability of certain lineages under climate change scenarios (Thuiller et al. 2011). This could be expected, since upper thermal physiological tolerances of species (which are one of the principal factors driving species range contractions) tend to be more similar in closely related species than in distantly related species (Araújo et al. 2013; Hoffmann et al. 2013). Therefore, species may show a non-random pattern of range contractions across phylogenies. However, this is not so evident (Comte et al. 2014); if no phylogenetic 'clustering' pattern is detected, and random or phylogenetic 'overdispersion' is shown, contractions may affect species indistinctly of their phylogenetic similarities. Similarly, if measures of species functional traits correlate with species expansions/contractions, this could indicate that some attributes present in certain species may be advantageous, or on the contrary detrimental, to their suitable habitat under climate change conditions (Buckley and Kingsolver 2012).

One of the most vulnerable ecological systems affected by the impacts of climate change are coral reefs (Parmesan 2006; Hoegh-Guldberg et al. 2007). The global distribution of these 'foundational' species (corals and hydrocorals) has varied slowly through geological time (Buzas and Culver 1994; Wood 1998), but recent environmental changes are causing an unusual and accelerated modification of their distribution patterns (Precht and Aronson 2004; Hoegh-Guldberg et al. 2007). In particular, some corals are being excluded from places under extreme hot temperatures, e.g. in some parts of the tropical Atlantic and Caribbean caused by bleaching events (Eakin et al. 2010), but they are also expanding their range to warming latitudes (Yamano et al. 2011). Climate projections can be used to detect the future magnitude of these changes in the distribution of corals (Couce et al. 2013), and concurrent phylogenetic analyses can elucidate if changes in the distribution of certain corals are phylogenetically constrained or not. To date, only one study has focused on how potential extinctions (based on IUCN criteria) will affect evolutionary diversity across the different reef ecoregions of the world (Huang and Roy 2015). However, whether the future shifts in corals' distribution are phylogenetically constrained or not, remains unexplored.

In this study, we used SDM techniques to predict the distributional shifts of 45 Atlantic scleractinian corals under a climate change scenario (A2 IPCC for the year 2100). We then explored whether these potential expansions, or contractions, are phylogenetically

and or functionally constrained. To reach this goal, we firstly assessed if distributional shifts (contractions/expansions) of 45 Atlantic reef-forming corals (scleractinian), and the main environmental variables driving their distributions, correlated with their phylogeny, i.e. whether expected contractions and expansions affected specific clades or not; and/or with coral functional traits. Secondly, we estimated the potential richness and phylogenetic diversity loss and/or gain across the Atlantic, as well as the phylogenetic structure (clustered/overdispersed/random) of the communities and the evolutionary distinctiveness of the species, resulting from these distributional shifts.

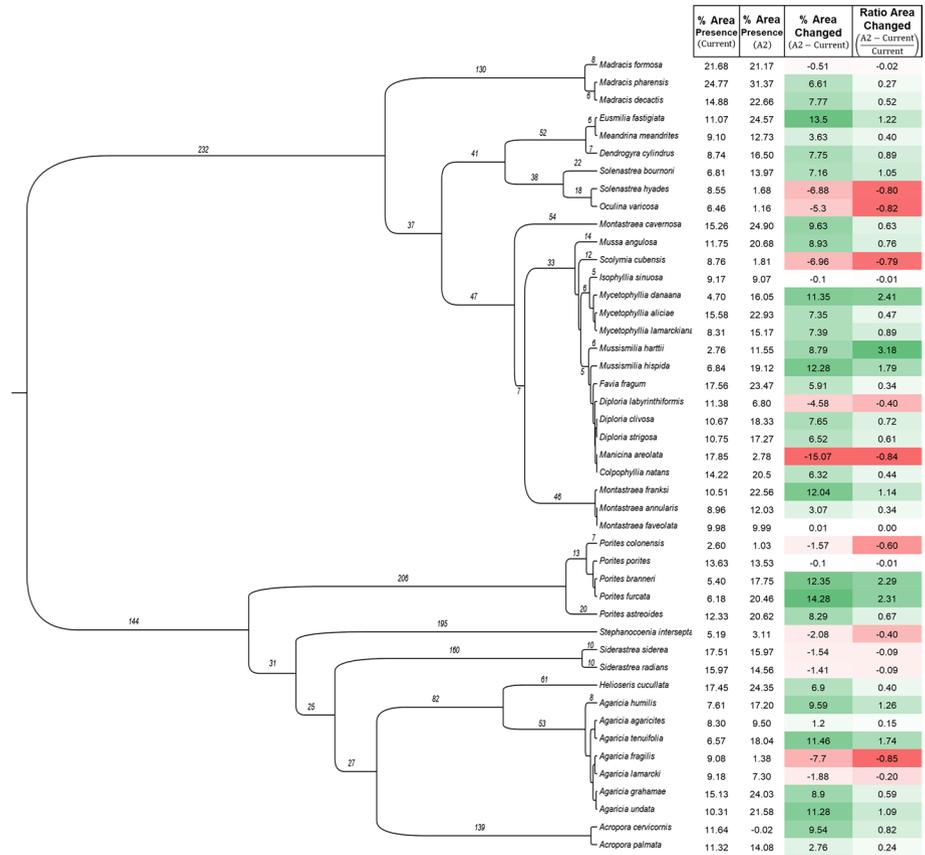
## Methods

### Species records

A review of Atlantic scleractinian corals was carried out through internet databases and books (Darling et al. 2012; Veron 2000; Veron et al. 2017: [www.coralsoftheworld.org/](http://www.coralsoftheworld.org/)). A search in the IUCN Red List was firstly filtered by the taxonomy (animal-cnidaria-anthozoa-scleractinia), and secondly by the location of the Atlantic FAO Marine Areas, including the northwest, southwest, western central and eastern central Atlantic. For these species, presence records were automatically downloaded using the R-Package “spocc” (Scott et al. 2017), an interface directly connected with occurrence data sources provided by the ‘Global Biodiversity Information Facility’ (‘GBIF’) and the ‘Ocean Biogeographic Information System’ (‘OBIS’). Presence records were checked with the literature available on coral distribution (e.g. Veron et al. 2017). Additionally, presence records were revised and, if necessary, edited by removing duplicates, fossil records or erroneous data. Presence records separated by less than a pixel (0.25 decimal degrees) were also removed. Species with < 15 presence records were excluded to avoid inaccurate SDMs (Stockwell and Peterson 2002; Califf et al. 2007; van Proosdij et al. 2016). A final set of 45 species, covering 64% of Atlantic scleractinian corals, from which phylogenetic information was also available, was finally used (Fig. 1).

### Environmental variables

Environmental data were downloaded, as raster layers, from the global marine data set ‘Bio-Oracle’ (Tyberghein et al. 2012), including minimal, maximal, mean and range values of sea surface temperature (Sst), dissolved oxygen, pH, salinity, Chlorophyll *a*, diffuse attenuation (Da), phosphate, nitrate, and photosynthetically active radiation (Par) (Table S1). The distribution area, where corals occurred, included all the American coasts and the Cape Verde Islands, was restricted by a bathymetric mask of 100 m to include all records, whereas all the variables were rescaled to a resolution of 0.25° to match the biotic resolution. To avoid auto-correlated variables, a Spearman’s correlation matrix was generated (Fig. S1a), and among the groups with  $r_s > |0.80|$ , the most important variables driving corals’ biogeography were selected (Kleypas et al. 1999; Couce et al. 2012). The predictors finally selected were: Damax, Parmax, pH, Phosphate, Salinity and Sstmean. Additionally, other exploratory analyses, as a cluster dendrogram based on a distance matrix, also dispersed between the same 6 variables, with a threshold of 0.20 (inversely proportional to the Spearman’s 0.80, Fig. S1b). Variance inflation factor (VIF) analyses, which measure the inflation of the unexplained variance as a consequence of correlation between variables



**Fig. 1** Phylogenetic tree of Atlantic corals. The numbers represent branch lengths (values <5 were omitted). For each species, the percentage of area categorized as presence in the current and the A2 scenarios, the percentage predicted by the SDMs (A2 – Current) of contracted (negative values, reddish) or expanded (positive values, greenish) areas, is indicated. The ratio of this change is also included, e.g. if the value is +2, this means that the future suitable area will be double of the current area. If the value is –1, the habitat suitable for the species will disappear in the future. Negative values are represented in red, positive values in green, and no change (zero) in white. (Color figure online)

(Belsley et al. 1980; Marx and Smith 1990), showed values <5.2, which are considered acceptable (Duque-Lazo et al. 2016). Therefore, the 6 variables were included as predictors in the SDMs.

**SDMs**

Forty-five SDMs, one for each coral species, were developed to project their ‘current’ and ‘future’ habitat suitability across the entire Atlantic. To generate the SDMs, the maximum entropy modelling software (MaxEnt) was used. MaxEnt is a machine learning approach that correlates presence records with environmental gradients, by selecting the statistical model that maximizes the Entropy of the species probability distributions (Phillips et al. 2006). MaxEnt (maximum entropy) is the most widely used tool when absence data is

not available. Response curves were fitted to be linear, quadratic and hinge. Extrapolations were allowed in the projections. The regularization and beta parameterization were explored choosing the default settings, since they represented the most reliable response curves to detect temperature thresholds after comparing a set of models. The final output of MaxEnt was a raster map, projecting the habitat suitability across the entire Atlantic, for each species (constructed under current and future conditions, see below).

To evaluate the performance of the models, an internal data-splitting validation was applied, using 70% of the presence points for training and the rest (30%) for testing. The predicted area under the curve (AUC) was the performance estimator of the model. This measure is provided by the receiver operating characteristic (ROC) curve from MaxEnt (DeLeo et al. 1990), which assess the sensitivity of the model as the fraction of presence records correctly classified as presences (true positives) against the fraction of absence areas incorrectly classified as presence (false positives) (Allouche et al. 2006). AUC values > 0.85 indicate a good discrimination power (Phillips et al. 2006).

The habitat suitability of each species was determined under 'current' and 'future' conditions. The 'current' variables contained mean monthly values from years 2002 to 2009; the 'future' variables were extracted from the UKMO-HadCM3 model for the year 2100, which represents the A2 scenario conditions defined by the IPCC. The A2 is the most severe scenario among those provided by 'Bio-Oracle', with projected increases of temperature of 2.6 °C and CO<sub>2</sub> emissions > 800 ppm until 2100 (Meehl et al. 2007). Only Sst-mean and Salinity A2 2100 IPCC projections were available by 'Bio-Oracle'. Therefore, for the predictions, these future variables were included as inputs of the SDM along with the remaining 'current' variables (Damax, Parmax, pH, Phosphate); we assumed, therefore, that their current values will be maintained in the future. Once the habitat suitability maps of all the species were generated, they were binarized into potential presence/absence areas accordingly to the maximum training sensitivity plus specificity logistic threshold (Liu et al. 2005; Cao et al. 2013), assuming no dispersion limitations. Relative percentages of absence and presence areas respecting the total area of study were calculated. Then, areas of expansion/contraction for each species were calculated by extracting the values of the 'future' distribution relative to the 'current' maps.

Simulated potential 'current' and 'future' coral communities were then constructed with the two binarized maps of habitat suitability ('current' and 'future'). These maps were transformed into two community matrices ('current' and 'future') with predicted species presence and absence for every pixel of their corresponding map. Species richness was calculated for each pixel of the 'current' and 'future' maps, and potential changes ('future'-'current') were also calculated.

## Phylogenetic and diversity analyses

A phylogenetic tree (in nexus format), including only the target species of our study, was obtained pruning the large coral molecular tree provided by Huang and Roy (2015), using the R-package 'ape' (Paradis and Schliep 2018). Then, the evolutionary distinctiveness (ED) (Isaac et al. 2007), i.e. the originality or evolutionary isolation of each species in the pruned tree, was computed with the 'evol.distinct' function ('equal.splits' option) of the R-package 'Picante' (Kembel et al. 2010). The pruned tree was then transformed into a cophenetic matrix of phylogenetic distances, by computing pairwise distances between each pair of tips, using tree branch lengths through the R-package 'ape'. By means of non-parametric Spearman correlations, we tested for the significance of correlations between dissimilarities matrices of

phylogenetic distances and expansion/contraction areas and the six main variables driving corals distribution, calculated by means of Euclidean distances. A total of 9999 permutations were computed to test for the statistical significance of correlations ( $\alpha=0.01$ ). Analogously, a matrix of five functional attributes (Table S2), including colony morphology (doomed, branching and plating), reproduction mode (spawner or brooder), colony size, wave exposure (protected, exposed or broad) and the depth distribution was obtained for each coral species. The categorical variables were firstly converted to dummy (numerical) variables. From normalized functional attributes, a matrix of Euclidean distances, between each pair of species, was subsequently obtained. By means of a Mantel test, we assessed whether functional similarities between species were connected with similarities (via Euclidean distances) between species according to the set of environmental variables (mean values across the entire range of each species). Similarly, we also tested, by means of a Mantel test, whether the extent of retraction/contraction areas of corals were connected with their functional similarities. These analyses were based on the R-package ‘BiodiversityR’ (Kindt and Coe 2005).

To understand potential changes in the evolutionary diversity of Atlantic coral communities under ‘future’ climatic projections, three phylogenetic metrics were computed. In particular, the Faith’s phylogenetic diversity (PD), the phylogenetic species variability (PSV) and the standardized PD ( $PD_{SES}$ ) of the coral community from each pixel, under ‘current’ and ‘future’ conditions, were estimated. The Faith’s PD accounts for the sum of all branch lengths connecting the species in a community (Faith 1992); it was calculated with the ‘pd.query’ function of the R-package ‘PhyloMeasures’ (Tsirogianis and Sandel 2017). The PSV quantifies the degree of relatedness among species in the community (Helmus et al. 2007); values near 1 indicate that taxa are poorly related, while values approaching 0 reflect that taxa are closely related. PSV was calculated with the ‘psv’ function of the R-package ‘picante’ (Kembel et al. 2010). Resulting values of PD and PSV were then projected into geographic maps of ‘current’ and ‘future’ climatic conditions, and their differences mathematically computed. The  $PD_{SES}$  compares the observed PD to null communities generated by randomizations (Webb et al. 2008) to infer the phylogenetic community structure (clustered, overdispersed or random), in this case for each pixel of the map. Significant positive  $PD_{SES}$  values indicate phylogenetic ‘overdispersion’; significant negative values denote phylogenetic ‘clustering’ (Kellar et al. 2015); non-significant values otherwise indicate a random phylogenetic structure. The ‘ses.pd’ function of the R-package ‘picante’ was used to compute this measure. Standardized effect sizes estimate the divergence between the observed phylogenetic distances versus those of mean null communities, divided by the standard deviation of the phylogenetic distances in the null data;  $PD_{SES} = \frac{[obs_{PD} - mean(null_{PD})]}{sd(null_{PD})}$  (Webb et al. 2002). The  $PD_{SES}$  and their associated observed z-score and p-values were calculated through 999 randomizations of the taxa labels across the tips of the phylogeny. Communities under phylogenetic ‘clustering’ had p-values  $< 0.025$ ; p-values  $> 0.975$  indicated ‘overdispersion’; p-values between 0.025 and 0.975 denote communities are phylogenetically random.

## Results

### SDMs

The two main environmental variables driving the distribution of species, which most frequently appeared in the models according to the percent contribution and permutation importance, were ‘Phosphate’ and ‘Sstmean’ (Table S3). The lowest training AUC value

from all the SDMs was 0.883 (Table S3), indicating a good performance for all modelled species. Thirty-one species, out of the 45, were predicted to expand their suitable habitat by the year 2100, under the A2 IPCC scenario (Figs. 1, S2). Eight species are predicted to expand their ranges by a percentage > 10%. *Porites furcata* would potentially have the highest future range expansion (14% of the total territory). The highest relative increment, with regard to current conditions, was predicted for *Mussismilia harttii*, from 2.8% ('current') to 11.5% ('future'), i.e. more than three times its current suitable habitat. This relative increase of habitat suitability does not indicate that this species may also suffer potential contractions in some areas. Most of the species (38 of the 45) show a contraction in the Caribbean Sea (Fig. S2), producing a gap in this area. However, this contraction is counterbalanced by 25 coral species (as indicated in the total percentage), as a result of the potential predicted expansions. Only five species, *Agaricia teunifolia*, *Diploria clivosa*, *Madracis pharensis*, *Mycetophyllia lamarckiana* and *Porites furcata* are predicted to expand their potential range in the Atlantic without suffering any range contraction in their current suitable habitat (Fig. S2). Just *Solenastrea bournoni* will not experience any change in its current habitat suitability index. On the contrary, 14 species were predicted to reduce the proportion of their current suitable habitat by 2100; *Manicina areolata* exceeded a 15% contraction of the total territory, reducing 84% of its current suitable habitat. *Agaricia fragilis* had the highest relative reduction, from 9.2% ('current') to 1.3% ('future'), so 85% of its current suitable habitat is predicted to disappear by the year 2100. This indicates that these species, as well as others such as *Oculina varicosa*, *Porites colonensis*, *Scolymia cubensis*, *Siderastrea radians* and *Solenastrea hyades*, will practically lose all their current suitable habitat by the year 2100 (see Fig. S2). According to the predictions, species richness will decrease in some tropical regions; notably in the Caribbean Sea, some regions of Brazil, as well as in the coasts of the Gulf of Guinea in Africa. Conversely, some areas between the Caribbean Sea and Brazil, along with some regions at higher latitudes in America and Africa, will increase their richness.

## Phylogenetic and trait-based analyses

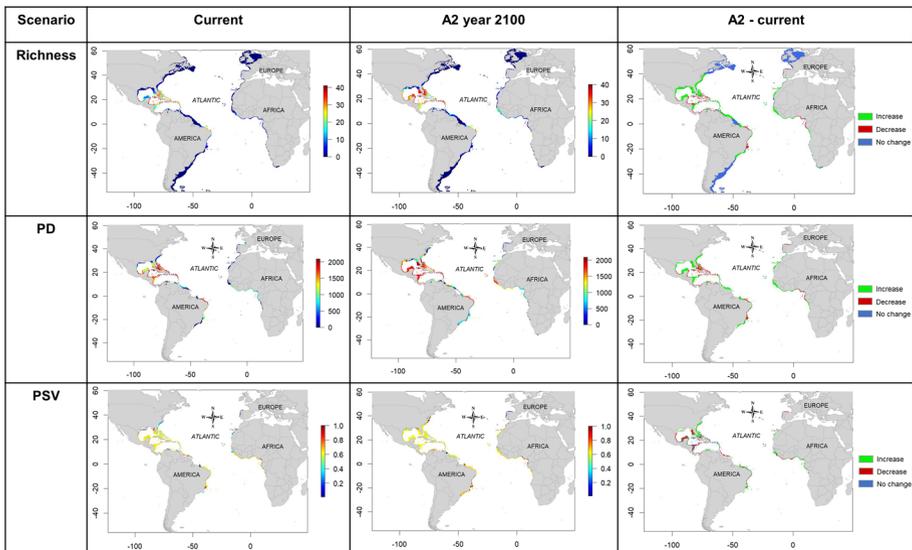
The Spearman correlation between dissimilarity matrices of phylogenetic distances and expansion/retraction areas of corals was non-significant ( $\rho = -0.003$ ,  $p$  value > 0.2). As a result, predicted distributional shifts of corals are independent of their phylogenetic relationships. These shifts appeared randomly distributed across the phylogeny (Fig. 1); unrelated species exhibited similar habitat changes relative to closely related species. Similarly, variables driving the distribution of the species showed un-significant correlations with the dissimilarity matrix of phylogenetic distances (Table S4). Similar results were also obtained for the functional traits and their relationships with the predicted areas of expansion/retractions of corals and with the environmental variables. The extent of expansion/contraction areas of corals were not connected with their functional similarities ( $\rho = 0.038$ ,  $p > 0.1$ ). And the functional similarities between corals were also not connected with the way corals are environmentally determined across their ranges (Table S5).

The change of PD from 'current' conditions to the year 2100 varied across the Atlantic (Fig. 2). Areas of increased PD coincided with areas where most species were projected to expand their ranges, e.g. most of the Gulf of Mexico, Florida (EEUU) and the North-western coast of Africa. Areas of decreased PD partially coincided with areas of decreased species richness (Caribbean, Brazil, Gulf of Guinea, Fig. 2), probably due to hot future temperatures (Fig. S3). A few exceptions included Nicaragua, The Bahamas

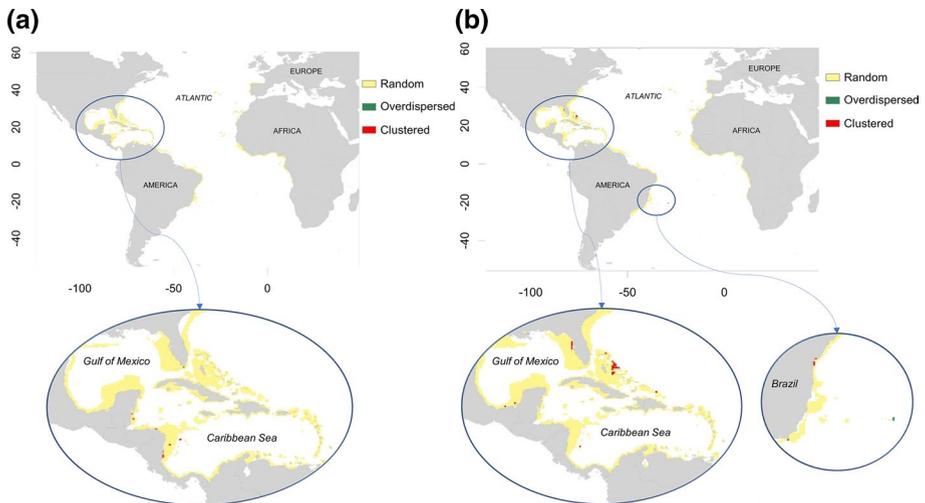
and nearby islands, where the species richness increased, but the PD decreased. This was due to loss of few species with long internal branches (e.g. *Stephanocoenia intersepta*, a species with few close relatives, presenting the highest evolutionary distinctiveness, ED = 246.4, Table S6), and the gain of more species with short external branches (e.g. *Mycetophyllia aliciae*, ED < 5).

The PSV index majorly decreased in West Florida, the Gulf of Mexico, Cuba, Haiti, Honduras, Nicaragua, Panamá, half of north Colombia, the Guyanas and Surinam, eastern Brazil, most of the Macaronesian islands, Sierra Leona, Liberia and Ghana. On the contrary, North and East Florida, Bahamas, the north of the Gulf of Mexico, North of Costa Rica, the other half of Colombia, Venezuela, the Lesser Antilles, some patches in Brazil, the western Canary Islands, Sahara, Guinea and the Gulf of Guinea increased their PSV. The rest of the areas maintained similar patterns of PSV under the A2 scenario relative to the current conditions.

Under ‘current’ conditions, only 0.25% of the pixels containing more than one coral species were phylogenetically clustered ( $PD_{SES} p < 0.025$ ) (Fig. 3), while only one pixel (i.e. 0.03% of the pixels) was phylogenetically overdispersed ( $PD_{SES} p > 0.975$ ). The rest of the pixels showed a random phylogenetic structure ( $PD_{SES} 0.025 < p < 0.975$ ). The results for the A2 scenario showed a slightly higher percentage of phylogenetically clustered (0.65%) and overdispersed pixels (0.15%). However, this still represents a very small portion (Fig. 3), indicating that most of the communities have a random phylogenetic structure.



**Fig. 2** Maps of evolutionary diversity of corals under ‘current’ (first column) and the A2 scenarios (second column). The third column shows changes from ‘current’ to ‘future’ conditions. Blue, green and red areas denote: no changes, increases and decreases, respectively, in the corresponding metric of diversity (species richness, PD and PSV). (Color figure online)



**Fig. 3** Phylogenetic structure of coral communities under the **a** 'current' and **b** 'A2' scenarios. Areas considered as 'phylogenetically random' are in yellow, 'phylogenetically clustered' in red, and 'phylogenetically overdispersed' in green. (Color figure online)

## Discussion

Our results have shown that 85% of the Atlantic corals (i.e. 38 out of 45) will decrease their suitable habitat in some regions, such as the Caribbean Sea, by the year 2100. This may cause their extinctions from those areas. From these species, 14 will suffer an absolute decrease in their total current suitable habitat by the year 2100, i.e. future habitat suitability will be lower than under current conditions (i.e. the future potential areas of contraction will be higher than any potential expansion). These species might be of high conservation interest, since they will drastically reduce their suitable habitat in the future. On the other hand, 82% (37 out of the 45 corals studied here) are predicted to increase their suitable habitat in some temperate regions; of course, if their dispersion capacities and competition abilities allow them to migrate and settle into those new areas (Occhipinti-Ambrogi 2007; van Gennip et al. 2017). Finally, 31 species, out of the 45, are predicted to expand their total range (i.e. the percentage of suitable habitat by the year 2100 will be higher than under current conditions). However, only five species are predicted to increase their habitat suitability without suffering any range contraction, so they can be considered the winners in the face of climate change. Despite the pattern of contractions differs among species, most species are projected to be contracted in tropical regions, coinciding with projected high temperatures in the future (Figs. S2 and S3). Similarly, potential expansions are expected to be located at higher latitudes, where current temperatures are too cold for corals; but due to global warming, temperatures will increase by the end of the century. These potential distributional shifts do not only affect the extinction risk of some coral species, but also change the species composition of these assemblages. Changes in the species richness and phylogenetic diversity of corals across the Atlantic show how climate change can distinctly disturb their current diversity pattern, i.e. decreases in tropical areas and increases at high latitudes. These changes have important implications for the preservation of coral assemblages, and the

results presented here can help to set priority areas of conservation (Huang and Roy 2015).

The two most important variables driving the distribution of Atlantic corals were ‘Stt-mean’ and ‘Phosphate’. These variables are directly connected with typical tropical conditions (Kleypas et al. 1999), because low phosphate levels (~0.1) enhance corals’ symbiosis, and low (< 16 °C) and high temperatures (> 30 °C) limit the photosynthesis of corals’ symbiont (Coles and Jokiel 1977; Glynn and D’Croze 1990; Hoegh-Guldberg 1999; Kleypas et al. 1999). However, beyond this general range of values, each species has slightly different preferences or tolerances, also depending on their location and their type of symbionts. Some species bleach at higher temperatures than others (Yee et al. 2008); e.g., branching corals are less resistant to bleaching than massive and encrusting corals (Loya et al. 2001). Since environmental tolerances vary across species, it is expected that phylogenetically related species would share similar environmental variation (Sunday et al. 2012). However, according to our results, there was not such phylogenetic connection. This may indicate that the stochasticity of the environment is more relevant than any constrained effect according to the phylogenetic topology. Similarly, no correlation was found between projected distributional shifts of Atlantic corals and their phylogenetic relationships. Nearly all the communities across the Atlantic showed a random phylogenetic structure, as well as intermediate relatedness values (PSV). In summary, any potential retraction will not explicitly affect certain clades of coral species. In other words, the potential future loss of Atlantic corals will be randomly distributed across the phylogeny, alleviating an inordinate loss of evolutionary history (Nee and May 1997; Heard and Mooers 2000; Mace et al. 2003; Thuiller et al. 2011). The lack of functional influences may be explained by the lack of a consistent quantitative functional framework for corals. It is well known that the way functional attributes are defined and quantified affects the identification of ecological patterns (Legras et al. 2019).

The species whose habitats are going to decrease the most are: *Agaricia fragilis* and *Manicina areolata*. According to the IUCN, *Agaricia fragilis* has not enough information to be categorized under any conservation status (i.e. a data deficient species), while *Manicina areolata* is considered as ‘least concern’. The evolutionary distinctiveness provided by our study sets *M. areolata* as the second species with the lowest score (ranking 44/45) and *A. fragilis* in the rank 32/45. This measure is often used to set conservation actions (Redding and Mooers 2006; Isaac et al. 2007); species with high values are prioritized in terms of conservation (more distinct), whereas species with low values are left in the background. Additionally, both species are considered as ‘weedy’ (Darling et al. 2012), which means they have high rates of growth and are prone to survive in non-favourable environments (Jackson and Hughes 1985; Darling et al. 2012). In view of this, both species would not be considered as priority species for conservation. However, our results project a severe decline in their habitat; additionally, they have also experienced relevant decreases during the last decades. For example, *A. fragilis* decreased a 53% from 1975 to 1982 in Florida (Dustan and Halas 1987). Rodríguez-Martínez et al. (2012) also reported a 9% decrease of *A. fragilis* colonies in the Mexican Caribbean reefs from 2006 to 2009. Other studies have informed about extensive bleaching impacts on both species; for example, in Bahamas, in 1998, 40% of the colonies of *M. areolata* were affected by bleaching (Mcgrath and Smith 2003). In Puerto Rico, *M. areolata* and *A. fragilis* suffered a severe bleaching event in 2005, which impacted the 100% of their colonies (Hernández-Delgado et al. 2006). These species might not be the most relevant from a distinctiveness perspective, but they are in decline, and, at least, they should be considered in future conservation decisions for the Atlantic. On the contrary, *Mussismilia harttii* and *Pories furcata* are two species, whose

area of expansion will potentially increase by the 2100. These corals can be considered as 'winners' under future climatic scenarios, as long as their dispersal capacity allow them to reach new areas.

Interestingly, our study shows different patterns of diversity changes caused by climate change depending on the metrics. Remarkably, the areas with larger changes in coral richness do not exactly coincide with those of larger PD changes. Richness and PD maps show certain differences in Bahamas, South and East of Dominican Republic, Puerto Rico, and the northern Lesser Antilles, where richness increases, but PD decreases. Despite richness increases there, lost species have long internal branches, which caused a higher decrease of PD than the relatively small increase produced by the incorporation of new, but phylogenetically similar, species. For example, in the south of the Dominican Republic, species that are predicted to appear in the future scenario are species closely related to those that are predicted to persist under future conditions (Fig. S4). The appearance of *Agaricia teunifolia* slightly increases PD, because it is closely related to *Agaricia agaricites*, which is present under both scenarios. Something similar occurs with *Porites branneri*, relative to *Porties furcata*. Likewise, the disappearance of *Manicina areolata* is practically imperceptible due to the persistence of a closely related species, *Colpophyllia natans*, both with very low evolutionary distinctiveness (ED). On the contrary, *Stephanocoenia intersepta*, present in the current scenario but absent under future predictions, lead to a relevant PD loss (Fig. S4). This species belongs to an isolated and old clade with no closely related species, showing high ED (Table S6). The large ED of *S. intersepta* suggests its pre-eminent conservation worth, because this is a unique species, which has no other phylogenetically similar relative if becoming extinct (Wilson 1992). Therefore, active conservation and restoration strategies, e.g. gene banks, artificial reefs via corals fragmentation, sexual assisted reproduction or transplantation (Young et al. 2012; van Oppen et al. 2015), will help to conserve this species and will avoid huge diversity losses in the future. On the other hand, the species shifts in this region produced an overall positive change in the PSV (Fig. 2), showing that the global relatedness of the species decreased with respect the current conditions. However, the future absolute values still represent no relevant relatedness among species.

Some areas show a decay in the projected PD, which is accompanied with a loss in PSV (e.g. Cuba, Jamaica, Haiti, Panama, and a small inner part of the Gulf of Mexico). In such areas, the removal of unique long branches is responsible for the main loss of PD; the elimination of short branches from one specific section of the phylogenetic tree causes a concurrent PSV decay (Huang and Roy 2015). These zones tend to display high mean sea surface temperatures, where physiological thermal thresholds of some corals can be exceeded, e.g. *Millepora alicornis* (Rodríguez et al. 2019); and future predictions of bleaching episodes are elevated (Donner et al. 2005; van Hooidonk et al. 2013; Huang and Roy 2015). Therefore, these geographical areas are of high vulnerability to climate change and thus of special interest for conservation.

Despite some relevant results obtained by this study, specially from a conservation perspective, some limitations need to be considered. Physiological thresholds in future conditions might be undetected by the MaxEnt response curves, so the use of Hybrid SMDs (see, Rodríguez et al. 2019) would be recommendable. The model is constructed only with presence data, and real absence data would improve confidence. This is particularly pertinent in areas where sampling effort is low, e.g. on the coasts of Africa. This is of special interest when generating the matrices of species composition for the diversity analyses, because the threshold chosen for making binary predictions can produce an overprediction in species richness (Dubuis et al. 2011; Benito et al. 2013; Schmitt et al. 2017). SDM

maps are based on habitat suitability indices, which do not assure that a species is currently present in an area, because of biotic factors, e.g. dispersal capacity, or competence with other species. This is the case of northern Spain, which is projected as a suitable area for the presence of some corals, although this region is currently habited by macroalgae, one of the main corals' competitors. Nonetheless, the cover of frondose, erect, macroalgae in northern Spain is currently (and projected to be) in decline due to warming temperatures (Martínez et al. 2012; Duarte et al. 2013; Martínez et al. 2015; Franco et al. 2017), so this opens an opportunity for tropical corals to compete if they reach these latitudes within the next decades, via ocean currents or anthropic routes of dispersion. The inclusion of dispersal corridors and species dependencies that are responsible for any spreading process would also improve our results (Hastings et al. 2005; Bowler et al. 2015; van Gennip et al. 2017). In this sense, the tropical hydrocoral *Millepora alcicornis* arrived to the Canary Islands in the last decade (Clemente et al. 2010), which according to some predictions could also expand its range to higher latitudes (Rodríguez et al. 2019). Hence, we must be aware that the use of SDMs have some limitations, but these tools are still useful when no field samplings are available and future projections are needed, generating relevant information at broad scales.

In summary, the richness and the phylogenetic diversity of the Atlantic coral assemblages studied in this research are predicted to change by the effects of climate change. In the future, some Atlantic areas could lose a considerable amount of richness and PD, particularly in the Caribbean, the central coast of Brazil and the Gulf of Guinea. However, other areas, mostly at higher latitudes and the western African coasts, could increase such richness and PD. The areas in decline can be considered as priority areas for conservation, which are usually affected by bleaching events, e.g. central Caribbean (Winter et al. 1998; Eakin et al. 2010). As previously mentioned for the conservation of unique species, assisted evolution could help to conserve these critical areas by building corals resilience (van Oppen et al. 2015). However, despite certain regions may lose many species (richness decrease), if the total length of the phylogenetic branches lost is small, the negative effect can be offset by the inclusion of new species with longer branch lengths. Notably, some species, as *Stephanocoenia intersepta*, when disappear from an area, contribute more to a quantitative decrease of PD because they belong to isolated old clades (high ED), than relatively young and redundant species. Conservation of such critical species can help to preserve the diversity of certain communities, if remaining species do not suffer a massive decline. Conservation efforts can also be focused on species with low ED (e.g. *Colpophyllia natans* or *Manicina areolata*), because they are able to regenerate novel diversity rapidly (Erwin 1991; Crozier 1997; Isaac et al. 2007). Detection of potential areas of significant loss of phylogenetic diversity, under climate change scenarios, is crucial to evaluate and protect the future of coral reefs.

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