

Integration of physiological knowledge into hybrid species distribution modelling to improve forecast of distributional shifts of tropical corals

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Abstract

Aim: Predicting species distributional shifts in future climate scenarios representing conditions that do not exist in the current world is a challenge. Species distribution models may result in misrepresented projections for species living in extreme conditions if based on truncated response functions. Model extrapolation may not detect declines that could occur if future environment conditions exceeded the physiological tolerance of the species. We developed a novel method aimed to overcome this constrain by incorporating the physiological response function of a tropical hydrocoral to temperature as a predictor variable in a Hybrid SDM.

Location: Atlantic Ocean.

Methods: We conducted ecophysiological experiments simulating heat and cold stress to determine the maximum photochemical efficiency of the hydrocoral's symbiont along a thermal gradient to identify sublethal and lethal conditions. The response curve obtained was then applied to a temperature raster to create a new physio-climatic variable, which was integrated into the Hybrid SDM as a predictor. Simple Physiological and Correlative SDMs were compared with the Hybrid model.

Results: The Hybrid SDM outperformed the Correlative SDM allowing predictions without extrapolations in the physio-climatic predictor. It suggested habitat contractions in tropical regions with forecasted temperatures above the coral's physiological tolerance, which were underrepresented by the Correlative SDM. It also incorporated habitat suitability restrictions by other predictors of unknown physiological response by incorporating correlative information (as limitations in river mouths by low salinity). In this way, by integrating mechanistic and correlative knowledge, the Hybrid SDM also predicted a potential expansion to higher latitudes, which agreed with the recent evidence of its expansion into the subtropical Canary Islands.

Main conclusion: Integrating physiological knowledge into Hybrid SDMs by adding a physio-climatic predictor improves model transferability resulting in predictions of decline in future climates, which may be misrepresented by SDMs trained at present-day conditions, and therefore are advisable for early warning in conservation management.

KEYWORDS

climate change, conservation, ecophysiology, hybrid species distribution models, marine biodiversity, *Millepora alcicornis*

1 | INTRODUCTION

Global warming is driving rapid shifts in the distribution of species worldwide (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). Our ability to accurately predict these changes allows a realistic forecast of potential retractions and expansions in the distributional ranges of species. Species distribution models (SDMs) are powerful predictive tools that consider the correlations between the actual distributional records of organisms and the environmental variables that control their distribution, estimating the habitat suitability for a species along existing environmental gradients (Guisan et al., 2013; Pearson & Dawson, 2003). SDMs can generate projections at different spatial and temporal scales by extrapolating species responses into future or past climatic scenarios (Franklin & Miller, 2010). Hence, these tools have been employed for predicting the probability of extinction of various taxa in several regions of the world, for example, plants, birds and frogs (e.g., Thomas et al., 2004), the spread of invasive species (e.g., Václavík & Meentemeyer, 2012), and for identifying potential climatic refugia under adverse scenarios (e.g., Martínez, Viejo, Carreño, & Aranda, 2012). SDMs have also been used to support conservation planning decisions (e.g., Guisan et al., 2013), such as the creation of new protected areas (e.g., Leathwick et al., 2008).

SDMs have many applications but they also have important limitations, especially when making projections for new regions or future climates (Elith & Leathwick, 2009; Thuiller, Brotons, Araújo, & Lavorel, 2004). Uncertainty increases when the species' responses to the climatic predictors need to be extrapolated to higher or lower values than the environmental gradient where the model was trained, in some cases because future conditions are uncommon or do not currently exist. In these projections, some statistical methods keep as a constant the last suitability value obtained from model predictors, for example, clamping in maximum entropy modelling (MaxEnt; Phillips, Anderson, & Schapire, 2006), whereas others extrapolate suitability as the last trend of the predictor response curve. When last suitability value is relatively high or trend is increasing, projections may fail by classifying as suitable regions where the projected environmental conditions will exceed the physiological tolerance for species survival (Anderson, 2013). Approximately 15 different correlative techniques are used in SDMs, such as random forests (RF), MaxEnt or generalized linear models (GLMs), but none of them can deal with this problem because they do not include specific terms incorporating the biological mechanisms driving the distributional limits of species (Buckley, Waaser, MacLean, & Fox, 2011; Martínez, Arenas, Trilla, Viejo, & Carreño, 2015).

Characterizing the physiological responses of species to climate and physical stress is the mechanistic basis for modelling their geographic distribution, including SDMs (Bozinovic, Calosi, & Spicer,

2011; Kearney & Porter, 2009). To investigate the mechanisms that explain tolerance limits, experiments that simulate stress conditions have been used routinely to obtain species response functions. These functions represent the physiological state of an organism along an environmental gradient including future conditions that do not currently exist. After obtaining the response curve, the species' threshold for survival can be determined and applied to the map of the physical variable, thereby predicting whether a species may become extinct under different climatic scenarios if the tolerance threshold is exceeded (Deutsch et al., 2008), but this modelling approach standing alone seems uncertain (e.g., Martínez et al., 2015). Only few studies have attempted to compare correlative SDMs projections with either those that apply thermal thresholds (Diamons et al., 2012; Gerick, Munshaw, Palen, Combes, & O'Regan, 2014; Martínez et al., 2015), biophysical models (Kearney & Porter, 2004; Kearney, Porter, Williams, Ritchie, & Hoffmann, 2009), process-based models (Morin & Thuiller, 2009) or physiologically models of extinction (Ceia-Hasse, Sinervo, Vicente, & Pereira, 2014). For example, Hijmans and Graham (2006) compared the predictions obtained by a mechanistic model after translating physiological information for 100 plant species into suitability indices, with those from SDMs. This and similar studies of trees by Austin, Smith, Van Niel, and Wellington (2009), beetles by Sánchez-Fernández, Aragón, Bilton, and Lobo (2012), and seaweeds by Martínez et al. (2015) found significant correlations between upper and lower thermal tolerance limits observed in experiments and response curves built from SDMs. Therefore, it seems reasonable to support the mathematical integration of both approaches (mechanistic and correlative) in the so-called Hybrid SDMs that has emerged just recently (see Dormann et al., 2012, and references therein). Albeit possible, Hybrid Modelling is uncommon and complex (see Talluto et al., 2016). One potential method outlined and developed by Elith, Kearney, and Phillips (2010) for toads, and similarly applied by Buckley et al. (2011) and Mathewson et al. (2016) for butterflies and the American pika, respectively, proposes using the output of a mechanistic model as the input layer into a correlative SDM. In line with this research, we develop one of the few examples of a physiologically based Hybrid Distribution Model, specifically incorporating a new physio-climatic predictor into the model of a marine tropical hydrocoral. This approach allows realistic predictions in future climate scenarios non-analogous to present-day conditions.

Tropical coral reefs are among the most diverse marine ecosystems throughout the world but also one of the most vulnerable to climate change (Hoegh-Guldberg, 1999). One-third of reef-building corals are considered to be at risk of extinction (Carpenter et al., 2008). Impacts on the foundational species that define the community structure (corals and hydrocorals) can lead

to large-scale losses of global biodiversity (Carpenter et al., 2008). Seawater temperature seems to be the main driver of coral biogeography, controlling many physiological processes that affect the normal functioning of corals such as respiration and calcification. Low temperatures, below $\sim 16^{\circ}\text{C}$, cause internal damage to the photosynthetic apparatus of the symbiont inducing the mortality of the coral (Saxby, Dennison, & Hoegh-guldberg, 2003). These temperatures are usually associated with high latitudes restricting the distribution of tropical corals to those limits. On the other hand, at the central areas of their distribution, corals live close to their upper thermal limit, thus high water temperatures may drive bleaching events involving the loss of symbiotic algae, which may ultimately cause their death (Douglas, 2003). Global warming has caused unusual and accelerated modifications of the geographic distributions of tropical corals, by leaving vacated regions with extremely hot temperatures, as in some parts of the Australian Great Barrier Reef, where some degree of bleaching affected 93% of corals (Hughes, Steffen, & Rice, 2016). On the other hand, poleward shifts of tropical currents that transfer warm conditions to subtropical and temperate latitudes are allowing corals to expand their ranges (Yamano, Sugihara, & Nomura, 2011). In particular, the hydrocoral *Millepora alcicornis* (Linnaeus, 1758) has recently established in the Canary Islands (Macaronesia), far north of its tropical distribution (Clemente et al., 2010), possibly by means of drifting material from the Caribbean Sea (Jokiel, 1989; López, Clemente, Almeida, Brito, & Hernández, 2015). Due to its stony skeleton and fast growth, this structural species (Huston & Huston, 1994) constructs a framework that serves as habitat for hundreds of tropical marine organisms in its native range (Lewis, 2006).

The aim of this study was to obtain a realistic prediction of the future habitat suitability of *M. alcicornis* under climate change scenarios representing conditions that do not currently exist. We developed a Hybrid SDM by integrating physiological information into a Correlative SDM and compared its results with those obtained using only a Correlative model on the one hand, and a Physiological model on the other. We hypothesize that the potential area inhabited by *M. alcicornis* will increase to occupy higher latitudes due to global ocean warming. Besides, a range retraction is also expected in tropical areas where future temperatures will feasibly exceed the thermal tolerance of this hydrocoral. We anticipate that only models fed with physiological information will be able to predict such retractions in distributional ranges, representing early warning tools for conservation management. First, we conducted physiological experiments by simulating heat and cold stress to obtain a thermal response curve for *M. alcicornis*. The bell-shaped response curve obtained was then applied to a temperature raster to create a new physio-climatic predictor, which was integrated into the Hybrid SDM. Finally, we projected the Hybrid SDM using the conditions of IPCC scenarios (year 2100) and compared the results with the current model to detect changes in habitat suitability. Our study demonstrates that projections obtained by correlative SDMs can be improved when physiological information about species is integrated by adding a physio-climatic variable to the list of predictors.

2 | METHODS

2.1 | Distributional records

Presence records for *M. alcicornis* were downloaded from the Global Biodiversity Information Facility (GBIF) and the Ocean Biogeographic Information System (OBIS) web portals. Additional presences were obtained from the scientific literature and from underwater videos kindly provided by the non-profit organization OCEANA. A total of 1,201 records were compiled, most (>90%) corresponding to observations taken from 1990 to 2011. Duplicate records and points less than 0.25° apart were removed using ArcGIS, to a final number of 159 reliable presences, that extended from Bermuda to the Brazilian coast of Rio de Janeiro in the western Atlantic Ocean, with maximal prevalence in the Caribbean islands, Ascension Island, and the coasts of Central America and Florida. Several presence records in the eastern Atlantic Ocean included the Cape Verde Islands, but no records were found on the African Coast (Figure 1a).

2.2 | Environmental predictors

To characterize the main environmental gradients in the ocean, we initially compiled 23 variables from Bio-ORACLE at 0.25° resolution (Tyberghein et al., 2012) (Supporting Information Table S1). All variables were restricted to a depth of 100 m to exclude ocean areas far outside the potential seabed habitat for the coral. To avoid excessive autocorrelation among the predictors, we selected for modelling a short list of variables with Spearman pairwise correlation coefficients <0.7 . We selected a set of six final predictors: Sstmean that controls most physiological processes, particularly bleaching (Coles & Jokiel, 1977; Douglas, 2003); Salinity, because corals have osmoregulatory limits (Berkelmans, Jones, & Schaffelke, 2012; Ferrier-Pagès, Gattuso, & Jaubert, 1999); Maximum photosynthetic active radiation (Parmax), which drives the photosynthetic response of the symbiont (Halldal, 1968); Maximum diffuse attenuation (Damax), as an estimator of the turbidity of the water column that decreases irradiance (Kirk, 2010) which impacts coral's health (Fabricius, 2005); Nitrate, as eutrophic waters increase bleaching effects (Koop et al., 2001); and pH, because decreases may cause the decalcification of reef-building corals (Anthony, Kline, & Dove, 2008).

2.3 | Correlative SDM

Presence records were linked to the final list of uncorrelated environmental variables using MaxEnt 3.3.3k. Background locations were randomly distributed using the *add samples to the background* setting of MaxEnt within the same extent of the environmental layers. Features were set to allow linear and quadratic responses, and the importance of each variable measured by the percentage contribution index (Phillips et al., 2006). As the choice of statistical modelling method may affect the selection of the significant predictors, we supplemented the variable selection from MaxEnt with two additional procedures: adjusting a GLM with "biomod2" based

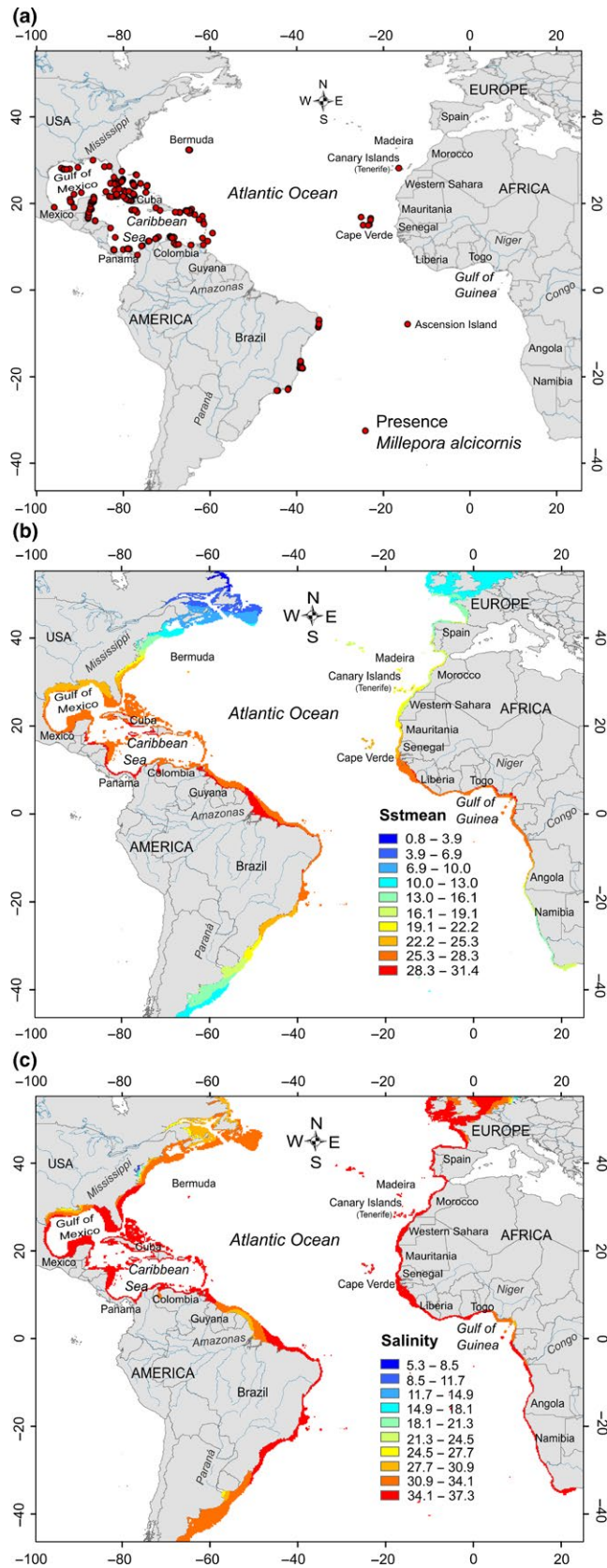


FIGURE 1 (a) *Millepora alcicornis* presence records in the Atlantic Ocean. (b) Mean sea surface temperature (Sstmean), and (c) Salinity maps downloaded from Bio-ORACLE (Tyberghein et al., 2012), restricted to a bathymetry of 100 m, and rescaled to 0.25° resolution

on pseudoabsences and quadratic terms, and then estimating the importance of each variable with the function `get_variables_importance` (Thuiller, Georges, & Engler, 2013); and using random forest (Kuhn, 2015), and the `importance` function (Liaw & Wiener, 2002). To create a consensus and parsimonious final model, we excluded the variables whose importance indices were below 20% in any of the three aforementioned approaches (Supporting Information Table S2). The final model including only two significant variables (see Section 3) was run in MaxEnt to project the habitat suitability in current and future scenarios, as this method has robust support for presence-only data (Elith et al., 2006).

2.4 | Functional response curve to temperature

Two experimental trails lasting 2 months each were done to determine the tolerance of *M. alcicornis* to cold and warm temperatures, respectively. The coral fragments (3–10 cm in height) provided by the Madrid Zoo Aquarium were pre-incubated indoors in a nursery tank for 1 month at 26°C by means of an automatic temperature control system (instrumental standard error of $\pm 0.5^\circ\text{C}$) and at 12:12 hr photoperiod. Water condition was maintained optimal throughout the pre-incubation and subsequent experimental trails: salinity = 34.4 ppt, pH = 8.0–8.6, alkalinity KH = 1.7–4.5, Calcium Ca^{2+} = 350–450 ppm, Magnesium Mg^{2+} = 1,200–1,400 ppm, and low concentrations of inorganic Nitrogen and Phosphorous ($\text{NO}_3^- < 0.25$ ppm, $\text{NO}_2^- < 0.3$ ppm, $\text{NH}_4^+ < 0.1$, $\text{PO}_4^{3-} < 0.5$ ppm).

Starting in March 2015, we tested the response to cold temperatures by placing 30 fragments in three independent 25-L tanks (10 per tank) and lowering the temperature by 2°C each week until reach lethal conditions. On May 2015, exactly the same experimental design was used in a second trial using 30 new fragments, but in this case, the temperature was increased in 2°C steps until death.

The maximal quantum yield of photosynthesis (F_v/F_m) using a pulse amplitude modulated (PAM) fluorimeter, after dark adaptation for 20 min., was measured in two replicate readings as a proxy of the maximum photochemical efficiency of photosystem II. Decreases in F_v/F_m are representative of physiological stress in endosymbiont algae (Maxwell & Johnson, 2000; Roth, 2014). Small background signals indicate the absence of coral symbionts but the presence of endolithic algae on the dead skeletons. The photosynthetic response to temperature was fitted using two logistic curves, corresponding to ascending and declining temperatures, linked by a stable plateau representing optimum levels (modified from Thornton & Lessem, 1978), with MATLAB software using the equation: $F_v/F_m(T) = \frac{a}{(1 + \exp(-b*(T-c))) * (1 + \exp(d*(T-e)))}$, where T is the temperature, a is the curve's maximum value, b is the slope of the ascending curve, c is the temperature value for the ascending sigmoid's mid-point, d is the slope of the descending curve, and e is the temperature value for the descending sigmoid's mid-point. Any potential tank effect was discarded by comparing the Akaike information criterion (AIC) for the models including versus excluding the tank factor (three per temperature) with the R packages "nlme" and "nlsm," respectively.

2.5 | Hybrid SDM

The bell-shaped curve relating Fv/Fm to temperature was applied to every pixel of the mean Sea Surface Temperature (Sstmean) raster to produce a new layer called "Yieldsstmean." Thus, we obtained a map reflecting potential Fv/Fm for every pixel. For example, a pixel of the raster Sstmean with a temperature value of 25°C was transformed into a potential Fv/Fm value of 0.588 in the new Yieldsstmean raster, suggesting optimal conditions, whereas too cold or warm conditions for coral survival both resulted in low values. This new physio-climatic variable was included as one predictor in the MaxEnt Hybrid SDM, as well as the Salinity layer, while other variables were found irrelevant (see Section 3). We then compared the: (a) the MaxEnt map modelled with the mentioned combination of the physio-climatic variable "Yieldsstmean" and Salinity as predictors (*Hybrid SDM*); (b) the MaxEnt map modelled with the environmental variables Sstmean and Salinity as predictors (*Correlative SDM*); and (c) the map generated by applying the physiological curve (Fv/Fm) to the variable Sstmean, that is, the map of "Yieldsstmean" (*Physiological model*).

We then binarized all the maps by dichotomizing the habitat suitability indexes using specific threshold values to represent potential presence/absence areas. The correlative and hybrid maps were binarized using the average of the "maximum test sensitivity plus specificity logistic threshold" obtained with MaxEnt from 10 model replicates. To binarize the Physiological model, an Fv/Fm threshold of 0.3 associated with the values for the descending and ascending sigmoid's mid-points (corresponding to 15.7 and 31.7°C, see Section 3) was applied to Yieldsstmean.

2.6 | Projections

We used the Correlative (Salinity and SSTmean) and Hybrid (Salinity and Yieldsstmean) SDMs trained with MaxEnt in the native area (American coast and Cape Verde Islands) to project the potential presence areas on the coasts of Western Africa (no available records), the Canary Islands (recent introduction) and Western Europe (absent). We applied the current conditions and three forecasted IPCC SRES scenarios based on the Coupled Model Intercomparison Project (CMIP3, Meehl et al., 2007): the B1 (stabilization of atmospheric CO₂ concentrations at 550 ppm), A1B (720 ppm stabilization) and A2 (most severe: 800 ppm) for 2100 as downloaded from Bio-ORACLE (Tyberghein et al., 2012). When predicting with the Hybrid model, we also applied the transformation using the physiological response curve to the SSTmean projected layers, obtaining three projected Yieldsstmean rasters (for B1, A1B and A2). Extrapolations were enabled with MaxEnt to allow projections in areas with environmental values outside the limits of the training data. The clamping function was also applied where extrapolated values were treated as if they were at the limit of the training range. Then, the areas where the projections fell outside the range of the training data were inspected using the most dissimilar variable (MoD) map provided by MaxEnt,

thereby indicating the variable furthest outside its training range (Elith et al., 2010). Regarding projections under the Physiological model, the physiological response curve (Fv/Fm) was applied to the Sstmean layers forecasted for the three IPCC scenarios, and then the maps binarized applying the Fv/Fm threshold of 0.3.

Four habitat categories arise by comparing current versus forecasted maps of habitat suitability: (a) presence: area categorized as presence in current and future scenarios; (b) absence: area categorized as absence in both scenarios; (c) new presence: area categorized as absence in the current scenario that changed to presence in the future scenario; and (d) new absence: area categorized as presence in the current scenario that changed to absence in the future scenario, representing a loss of suitable area. The areas corresponding to each category were transformed into percentages of the total studied area for the Hybrid, Correlative and Physiological models within the three scenarios of the IPCC (B1, A1B, A2) to allow comparisons (Supporting Information Table S3).

2.7 | Model evaluation

Models were assessed based on the current climatic scenario by calculating the Sensitivity (ratio of grid cells containing presence points correctly classified in presence areas), Specificity (ratio of pseudo-absences correctly classified in absence areas), Omission error (ratio of presence records wrongly classified) and Commission error (ratio of pseudoabsences wrongly classified) (Fielding & Bell, 1997). The "Correlative" and "Hybrid" models, both fitted by MaxEnt, were also tested using the regularized training gain (gain) and the area under the curve (AUC) of the receiver operating characteristic (ROC) plot as calculated by the MaxEnt software. The gain of the Physiological model was calculated using the function "gains" of the R package "gains," and the AUC using the function "auc" of the package "pROC" (Robin et al., 2011). Ten replicates of an internal data partitioning procedure (Fielding & Bell, 1997) were computed for the Correlative and Hybrid models by bootstrapping, where 70% of the points were randomly selected for training and 30% for validating. The geographic transferability performance was also assessed by partitioning the data using a geographic criterion, that is, data at the Northern Hemisphere (90% of presences) were used for training the model and those at the Southern Hemisphere (10%) for validating.

3 | RESULTS

3.1 | Correlative SDM

Among these six environmental predictors, only Sstmean and Salinity contributed more than 20% to the MaxEnt, GLM and random forest models and thus were the only used in projections (Supporting Information Table S2). The SDM response curves for these variables showed that Sstmean >30°C and Salinity >36 PSS produced high habitat suitability values (~0.7), whereas temperature <20°C and Salinity <33 PSS reduced the habitat suitability to a low level (~0.2) (Supporting Information Figure S1a).

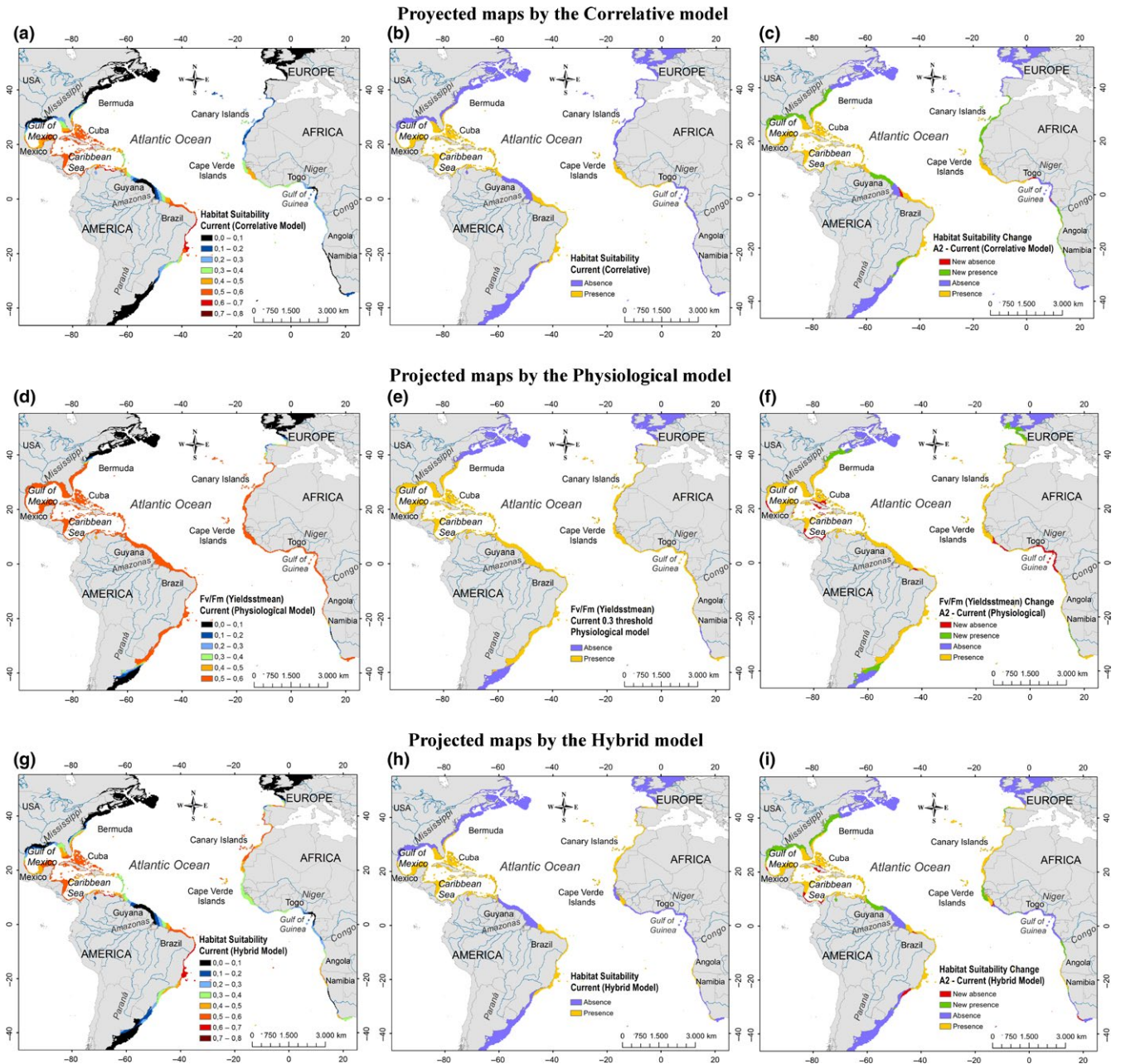


FIGURE 2 Projected maps of the habitat suitability of *Millepora alcicornis* in the Atlantic Ocean by applying the Correlative (a–c), Physiological (d–f) and Hybrid models (g–i), using 10 replicates in MaxEnt to obtain mean values for the Correlative and Hybrid models, and the physiological response curve in the Physiological model. The maps shown in the left column represent the habitat suitability projections (a and g) and the Fv/Fm (Yieldsstmean) (d) using the scenario of current climatic conditions. The maps in the central column were obtained binarizing those in the left column by applying the logistic threshold of Maximum Test Sensitivity Plus Specificity for habitat suitability (0.27 in b, and 0.29 in h); and the threshold Fv/Fm value of 0.3 in e; the blue colour indicates areas of potential presence and the black represents areas of potential absence. The maps in the right column show the potential changes in habitat suitability in the future climatic scenario of IPCC A2 compared to the binarized current scenario (central column), new areas of potential presence are in green and new areas of potential absence in red

After running MaxEnt with present-day layers of Sstmean and Salinity and binarizing the maps, that is, the Correlative SDM, the areas categorized as presence corresponded to the Gulf of Mexico, all the Caribbean Sea, the middle coast of Brazil and Cape Verde, which matched with the actual distribution of the species, but also the coasts of Guinea, Sierra Leone and Liberia with no presence

records (Figure 2a,b). In addition, the model classified as potential presence areas the westernmost islands of the Canary Islands, including Tenerife, where *M. alcicornis* was found recently (Clemente et al., 2010). The model correctly explained the current distribution of the species, and thus, Sensitivity was high (0.93, Table 1), as well as identified unexplored and potentially new presence areas on the

TABLE 1 Contingency validation table

	Correlative model		Physiological model	Hybrid model	
	Internal validation	Geographic transferability	Validation ^a	Internal validation	Geographic transferability
Sensitivity	0.93	0.90	1.00	0.88	0.92
Specificity	0.56	0.58	0.37	0.59	0.56
Omission error	0.07	0.10	0.00	0.12	0.08
Commission error	0.44	0.42	0.70	0.41	0.44
AUC-ROC ^b	0.83	0.85	0.59	0.81	0.95
Gain ^c	0.82	0.37	0.33	0.75	0.63

Note. Sensitivity and Specificity, calculated as the ratio of presence records and pseudoabsences correctly projected, respectively.

Omission and Commission errors, as presences and absences wrongly predicted, respectively. Results obtained by the three different models (Correlative, Physiological and Hybrid) are shown.

^aThe Physiological model had neither internal validation nor geographic transferability as not fitted using MaxEnt. ^bThe AUC-ROC of the Physiological model was developed using all the presences and the double of pseudoabsences. ^cThe gain for the Physiological model was obtained by the package "gains," whereas for the Correlative and Hybrid models the regularized training gains were obtained by MaxEnt.

African coasts. Most absence areas were also correctly classified comprising the northern coasts of the Gulf of Mexico, the coasts of Guyana, Surinam, French Guiana, north-south Brazil, and most African and European coasts (Figure 2b), due to the low salinity values in river mouths and the low temperatures at high latitudes (Figure 1b,c), resulting in fair Specificity (0.56, Table 1). These results were further supported by the geographic transferability validation obtaining similar Sensitivity and Specificity values (0.90 and 0.58, respectively, see "Correlative model" in Table 1).

Projected distributional patterns were similar among the three future scenarios (B1, A1B and A2) (compare Figure 2c and Supporting Information Figure S2a,b; and values in Table S3), and thus, the most severe future scenario (A2) is used to explain the results. The Correlative SDM, using the A2 scenario, predicted that 38.7% of the territory studied by the year 2100 will be represented by presence areas, of which 14.8% will become new presence areas relative to the current projection. This increase in the potential area of occupancy will be partially located on the coasts of USA, in the north of the Gulf of Mexico, on the coasts of Guyana and Surinam, on the coast of Angola and north of Namibia, from the coasts of Morocco to Senegal, and the eastern islands of the Canary Islands, Madeira and south of Spain. On the other side, new contractions comprising small new absence areas were evident in the north of Brazil, as well as in Togo and Benin representing 0.9% of the territory (Figure 2c, Supporting Information Table S3).

3.2 | Physiological model

The estimates of the coefficients c and e in the bell-shaped response curve, that is, the temperature values for the mid-points of the ascending and descending sigmoid, were 15.7 and 31.7°C, respectively, suggesting rapid decreases in F_v/F_m below 0.3 at these two temperatures (Figure 3). Therefore, this threshold value was considered a good proxy of lethal conditions and, as mentioned, was applied to

the map of the physio-climatic predictor Yieldsstmean (Figure 2d) to estimate the potential areas of presence-absence (Figure 2e). When comparing this map with that from the Correlative SDM, high habitat suitability was suggested at latitudes between 40°N and 40°S overestimating the actual extent of the species, and thus, Sensitivity was 1, but Specificity the lowest among models (0.37, Table 1). Absence areas by low salinity conditions detected by the Correlative SDM were misclassified as this physiological response was not investigated experimentally (in this study or previously) and thus could not be considered.

The overestimation of presence areas by this model was also evident in the forecasted map for the IPCC scenario A2, where presence areas represented the 48.9% of the total territory (Supporting Information Table S3), including new presence areas to higher latitudes than those suggested by the Correlative SDM (compare Figure 2c,f), that would fall within the physiological thermal tolerance of the species when other limiting factors are not accounted for. On the other hand, the Physiological model predicted significant absence areas including much of the Gulf of Mexico, the Caribbean Sea and the Gulf of Guinea, suggesting forecasted situations of high lethal temperature conditions not detected by the Correlative SDM along the centre of distribution of *M. alcinornis*.

3.3 | Hybrid SDM

Yieldsstmean and Salinity were used in the Hybrid models because they contributed more than 20% to the MaxEnt algorithms (58.5% and 33.3%, respectively). When compared with the Correlative SDM, the potential presence areas suggested by the Hybrid approach for the current climate were almost the same for the American continent (compare Figure 2b,h) resulting in a similar Sensitivity (Table 1). On the other hand, larger presence areas were projected by the Hybrid SDM for the westernmost coasts of Africa and the Canary Islands, suggesting in these coast temperatures within the physiological

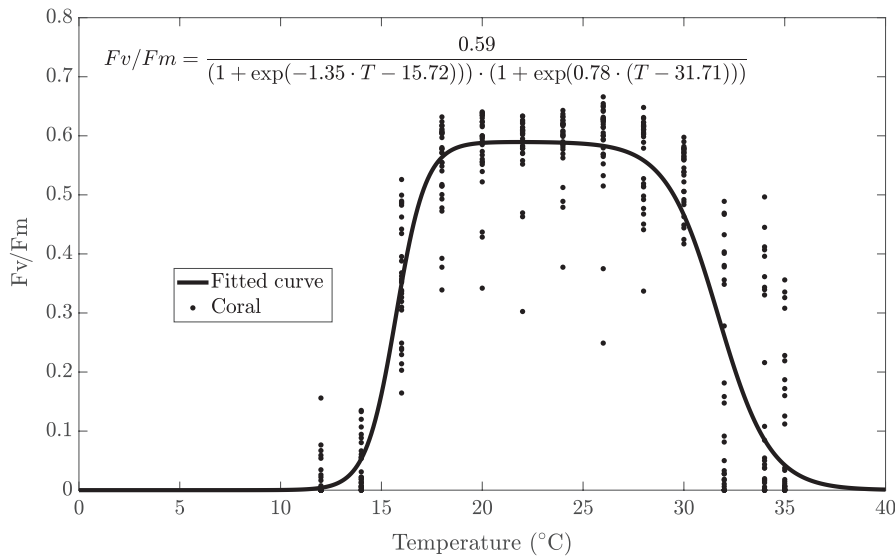


FIGURE 3 Response curve of the Maximal Quantum Yield of Photosynthesis (F_v/F_m) of *M. alcicornis* with temperature. The points indicate the F_v/F_m measurements for each coral fragment ($n = 30$) using a Pulse Amplification Fluorometer (PAM). The line represents the fitted curve: $F_v/F_m = a / ((1 + \exp(-b \cdot (T - c))) \cdot (1 + \exp(d \cdot (T - e))))$ ($R^2 = 0.82$), where T represents the temperature, and the coefficients (95% confidence intervals) are as follows: $a = 0.5899$ (0.5719, 0.6078), $b = 1.346$ (0.9843, 1.707), $c = 15.72$ (15.53, 15.91), $d = 0.7756$ (0.6392, 0.9119) and $e = 31.71$ (31.43, 31.98)

tolerance of the species detected in the experiment and incorporated in the model. In discrepancy with the Physiological model, but analogous to the Correlative SDM, the “Hybrid map” showed discontinued absences in areas of low salinity overlapping with the Mississippi, Amazon, Niger and Congo rivers. It incorporated the restriction to low salinity captured by the correlative approach, and thus, Specificity was similar between these two models, and higher than that of the Physiological model (Table 1).

For the future A2 scenario, 35.7% of the territory was estimated as presence area (Supporting Information Table S3). There were increases of new potential presence areas respect the current projections (12.0%, Supporting Information Table S3) on the inner eastern coasts of the USA, Guyana, Surinam, the northern coasts of Spain and Portugal, and the coasts of Senegal, Guinea and Namibia (Figure 2i). Tenerife still maintained the potential probability of presence in 2100, comparable to the expansion forecasted by the Correlative SDM (compare Figure 2c,i). Remarkably, potential new absence areas, mostly not captured by the Correlative SDM, expanded along the Caribbean Sea, Brazil, and a small spot by Sierra Leone, in response to predicted increases in seawater temperatures exceeding the species physiological threshold (Figure 2h,i). This resulted in an increase of 3.2% of new absence areas compared with the current projections and a sum of 64.3% of total absence areas for the year 2100 (Table S3).

3.4 | Models evaluation in current scenarios

Overall, all models correctly classified the current presence areas of *M. alcicornis*, which mostly extend along the tropical western Atlantic, thus showing high Sensitivity values (Table 1). However, models performed differently in classifying the absence areas of the species (mostly along the African coasts). The Physiological model based on the thermal threshold was different than the other two in classifying most of the territory of higher suitability from the present-day climatic conditions onwards and thus was of poor

Specificity and of high Commission error respect to the other two (Table 1).

The evaluation metrics for the two SDMs fitted with MaxEnt and based on random internal partitioning of presences (70:30) ranked the Correlative SDM somewhat better than the Hybrid in discriminating presence-absence areas by both the mean regularized training gain and AUC metrics (Table 1), although all values were indicative of correct model performance. On the contrary, the geographic transferability validation presented higher values of AUC for the Hybrid SDM (0.95) than for the Correlative SDM (0.85), as well as for the regularized training gain (0.63 and 0.37, respectively, Table 1), thus suggesting its better performance when the partitioning is done by a geographic criterion.

3.5 | Comparisons of predictions

Projected future environmental conditions largely exceed those in the training data (Sstmean $>31.5^\circ\text{C}$ and Salinity >37.3 PSS) for the three IPCC scenarios, and thus, extrapolations from independent models resulted in different predictions. The Correlative SDM extrapolated high suitability continuously to the maximum value set by the truncated response curve (mean temperatures $>31.5^\circ\text{C}$ were extrapolated to suitability values of 0.71, Supporting Information Figure S1). This is unrealistic because experimental results suggest decreased hydrocoral physiological performance at temperatures above 32°C (Figure 3). This was captured by the Hybrid and Physiological models when predicting large absences at the central distribution of the species in the future. Nevertheless, the Hybrid SDM also included the constraint by low salinity suggested by the distributional records, thereby allowing it to predict absences in river mouths outperforming the Physiological model (Figure 2i).

Regarding spatial bias in future projections, the MoD figure obtained by the Hybrid SDM (Figure 4b) indicated a smaller area of uncertainty in comparison with the Correlative SDM associated only with salinity values outside the training data (Figure 4a). In the

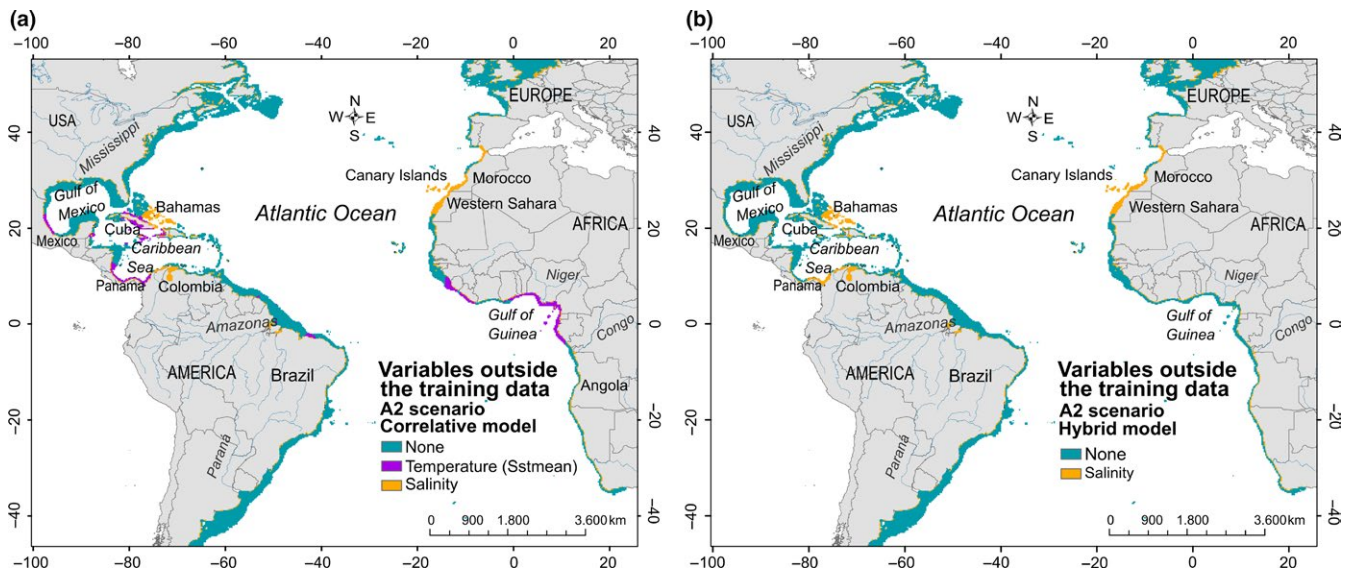


FIGURE 4 Most dissimilar variable (MoD) areas in the Atlantic Ocean where environmental predictors are extrapolated outside the training data when applying the A2 future climatic scenario to the distribution of *M. alcicornis*. Colours indicate the variable furthest outside the training range in (a) the Correlative model and (b) the Hybrid model. Extrapolations in Sstmean (in purple) extend along Cuba, Panama and Gulf of Guinea with the Correlative model. Under both models, extrapolations of Salinity (in orange) affect mostly the Bahamas, Colombia, Canary Islands and Morocco. Turquoise represents the areas not affected by variables outside the training data

Hybrid SDM, future non-analogous areas for the physio-climatic variable were null because the physiological response function was bell-shaped, and therefore, low values of the F_v/F_m ratio were achieved for two (cold and warm) current thermal conditions. Hence, the Hybrid model was trained at all possible values of F_v/F_m avoiding extrapolations in future climate scenarios (see the double scale on the right panel in Supporting Information Figure S1b). In summary, by reducing extrapolation, the Hybrid SDM suggested current unoccupied potential presence areas (e.g., Western Sahara and Angola), and possible future areas of absence not detected by the Correlative SDM (e.g., Cuba, Mexico or Gulf of Guinea), as it also captured the correlative information on Salinity unnoticed by the Physiological model.

4 | DISCUSSION

We provide in this study an improved and transferable method to predict distributional shifts of species in future environmental conditions that do not currently exist. This was achieved by integrating physiological knowledge into correlative SDMs to develop Hybrid SDMs, following the idea of using the output layers of a mechanistic model as the input layers for a correlative one (Buckley et al., 2011; Elith et al., 2010; Mathewson et al., 2016). We defined a physio-climatic predictor of thermal tolerance for the fire coral in each location by relating the thermal conditions at these sites, with the potential photosynthetic performance of its symbionts observed in experiments, which is closely related to their survival. This physio-climatic variable can be viewed as a transformation of the temperature layer into a meaningful raster for the physiology and survival of the coral.

Moreover, as this variable was an adequate predictor of habitat suitability, MaxEnt and other common modelling algorithms selected it as a major predictor for the Hybrid SDMs. Similar to the Correlative SDM, the Hybrid SDM also accounted for other important physical drivers (salinity in this study), as captured by the correlations between presence records and environmental layers. Although the Hybrid SDM did not outperform the Correlative SDM when the internal validation was applied to current climatic conditions, it did so in the geographic transferability assessment, and provided robust predictions for future climatic scenarios by reducing the areas of extrapolation to non-analogous climatic conditions. This is particularly interesting when forecasting the future fate of foundational corals and other tropical organisms, which are expected to withstand higher temperatures than current ones.

To build a Hybrid SDM, a physio-climatic variable can be defined and included as a predictor in the SDM (this study; Elith et al., 2010). This physio-climatic predictor should be a direct estimator of the survival of the species under a limiting environmental factor. If this is not possible, a physiological proxy of the organism's performance may be used, for example, oxygen consumption that assesses the metabolic rate in fishes (Cech & Brauner, 2011), net assimilation rates that indicate plant growth (Williams, 1946) or the F_v/F_m to assess the photosynthesis yield in photosynthetic organisms, as in this study (Maxwell & Johnson, 2000). This information can be obtained from previous ecophysiological studies, as summarized in new databases (e.g., Bennett et al., 2018). However, the description of the physiological response at all range of environmental conditions, that is, the bell-shaped double-logistic regression, is often unavailable, and its variation due to phenotypic plasticity and/or local adaptation is usually unknown (Valladares et al., 2014). After obtaining the

response function from literature or using experiments, it is applied to each pixel of the physical raster layer (Sstmean in this study) to obtain the physio-climatic predictor (Yieldsstmean). This new physio-climatic raster encompasses all the possible values of the variable because functions of vital traits are bell-shaped; therefore, the low values will result either from low or high physical conditions, whereas high values will result from optimum conditions. This allows training the Hybrid SDM in all possible values of the physio-climatic predictor, and therefore, extrapolations in this variable on projections are avoided. In this study, the low values of Fv/Fm expected for future warming scenarios were related to low habitat suitability by both too cold and too warm temperatures for the occurrence of the coral in the current climate. Finally, additional physical predictors (e.g., Salinity) can also be included into the Hybrid model, and then fitted and validated following standard procedures.

Hybrid SDMs can be readily applied to marine organisms with geographic ranges that typically conform better to their thermal physiological thresholds than terrestrial species (Sunday, Bates, & Dulvy, 2012). In addition, as the ocean temperature does not show large oscillations compared to atmospheric temperature (Kearney & Porter, 2009; Martínez et al., 2015), physiological information is easier to relate to averaged environmental data from satellite imagery (Smale & Wernberg, 2009). However, we do not exclude its generalization to terrestrial systems as environmental rasters are gaining meaning with respect to the physiology of organisms (Assis et al., 2018; Kearney, Isaac, & Porter, 2014). Similar approaches to improve SDMs predictions have been developed by several authors; for example, Elith et al. (2010) with toads, combining climatic variables and the output of a mechanistic model (Kearney et al., 2008). Also Buckley et al. (2011) with butterflies, using a predictor based on their lower developmental time. And Mathewson et al. (2016) that predicted the distribution of a terrestrial endotherm incorporating its predicted surface-activity time, obtained from Niche Mapper, into a SDM, to conveniently project the spatial variation of the species' thermoregulation response to future warming scenarios. The main difference of our proposed Hybrid SDM with these studies is that while they use mechanistic models based on modelling platforms, ours is based on empirical results which are direct measures of the organism' physiology.

When comparing the Physiological, Correlative and Hybrid models to determine the best option for predicting the geographic distribution of *M. alvicornis*, the Hybrid SDM had the best performance and overcame the disadvantages of the other two methods. The Physiological model clearly overestimated the presence areas, classifying in the current climate, the entire American and African coast from 40°N to 40°S as of presence, and omitting the absence areas in river mouths. This model represented well the potential thermal niche (sensu Jackson, Overpeck, Paleobiology, & Autumn, 2000), that is, the portion of the fundamental niche existing in the geographic space, but without considering other niche axes, resulted in the overestimation of the habitat (Martínez et al., 2015). The inclusion of other environmental constraints in the Hybrid SDM by incorporating the relationship with salinity (as in the correlative SDM) partially solved this restriction. This model projected a more realistic

expansion of *M. alvicornis* in regions of the African coast, according to the recent evidence of establishment of populations at higher latitudes in the Canary Islands (Clemente et al., 2010). It also accounted for the limits of the potential niche of thermal tolerance, which resulted in novel predictions of decline in the centre of distribution that were unnoticed by the extrapolations of the correlative SDM. This prediction is in concordance with the trend observed by tropical corals worldwide (see Section 1). In this way, hybrid models can help establish priority conservation areas in regions that would not be detected with correlated models, which represents an important tool for early warning systems (Keith et al., 2014).

The future projections of climatic conditions included values outside current levels, which will become common for corals, as they are tropical organisms living close to the hottest temperatures found in the ocean. As aforementioned, the Hybrid SDM reduced the uncertainty associated with future extrapolations. Descombes et al. (2015) solved the problem of inferring extrapolations by using Eocene coral fossil data and the corresponding climatic conditions (warmer than the IPPC scenarios) to describe the whole thermal response curve for corals, assuming that the fossil records correctly captured the entire environmental range limits of the species. However, if the fossil record is incomplete, and/or represents an unfilled niche, then our proposed Hybrid SDM can overcome these problems because it uses the fundamental thermal niche of ecophysiological tolerance. Anderson (2013) proposed this solution when the niche space assumption is violated, that is, when the study does not contain the full range of conditions that a species tolerates, and thus, the response curves are truncated. The results obtained with the Hybrid SDM showed a future decline in the areas where future temperatures will exceed the physiological thermal threshold of this species. At present, there is no similar mechanistic knowledge about Salinity, but it can be easily incorporated from additional experiments using our hybrid approach, as well as other relevant physio-climatic variables and emerging physiological knowledge.

According to Carpenter et al. (2008), corals are at higher risk of extinction due to climate change, where recurrent bleaching events are linked to the increase in sea surface temperatures (Hoegh-Guldberg, 1999), for example, a catastrophic event affected the Great Barrier Reef during 2016 (Hughes et al., 2016). The most feasible measure of bleaching is the photosynthetic efficiency (Fv/Fm), which is considered a good indicator of coral health (Roth, 2014). Under laboratory conditions, we found that *M. alvicornis* exhibited a suboptimal decrease in Fv/Fm and degraded health at temperatures below 16°C and above 32°C. Future projections under the A2 scenario indicate temperature increases that would exceed the physiological upper thermal tolerance limit for this species, mainly in the Caribbean Sea and Gulf of Mexico. However, these regions were not projected as areas with declines in habitat suitability for coral reefs by other studies based on SDMs using the same scenarios (see Couce, Ridgwell, & Hendy, 2013), which did not incorporated physiological knowledge. The upper thermal limits found in our study agreed with those that define potential areas of bleaching for scleractinian corals (Donner, Skirving, Little, Oppenheimer, & Hoegh-Gulberg, 2005), and with the

future hyper-tropical zone proposed by González-Duarte, Megina, López-González, and Galil, (2016), where mass mortalities are expected. The projected areas of decline determined by our Hybrid SDM represented 2.5% of the current suitable areas ($\sim 1.63 \times 10^7$ ha). If these projections are met, assuming there is no time for thermal adaptation and accounting that the most pessimistic temperature scenario is being used in this study, these areas will lose a key reef-forming species, which may lead to reef degradation, and loss of marine biodiversity and ecosystem services (Carpenter et al., 2008). The ability to detect areas potentially vulnerable to climate change, undetected by other methods, highlights again the importance of Hybrid SDMs as early warning tools for conservation management plans, for example, anticipating areas which need urgent conservation support (see Beger, Sommer, Harrison, Smith, & Pandolfi, 2014).

On the other side, due to seawater temperature increases (as those projected by the A2 scenario), this study predicted *M. alcicornis* spread to other subtropical and temperate areas of minimal temperature $>16^\circ\text{C}$, if allowed by its dispersal capacity and biotic interactions. The current presence of *M. alcicornis* in the Canary island of Tenerife already supports this fact. López et al. (2015) established the genetic origin of *M. alcicornis* as the Caribbean region from where it could have been rafted by the Gulf Stream (López et al., 2015). *M. alcicornis* is a pioneer species, which can provide habitat for other associated marine biota, such as tropical fish (Coni et al., 2013), which have already appeared in Tenerife (see Brito, Falcón, & Herrera, 2005), thereby indicating a potential tropicalization of this Archipelago. Poleward range expansions of tropical corals have already been reported worldwide (Greenstein & Pandolfi, 2008; Yamano et al., 2011), and although they may serve as a refuge against climate change effects, they could also cause ecological problems by out-competing native species that are currently in decline such as their temperate counterparts the macroalgae (Serrano, Coma, & Ribes, 2012; Vergés et al., 2014; Wernberg et al., 2016).

In summary, the potential distribution of *M. alcicornis* will expand to higher latitudes by the year 2100 and experience contractions in some tropical regions due to climate change. As suggested by Elith et al. (2010) and Buckley et al. (2011), and corroborated in this study, it is feasible to develop Hybrid SDMs integrating physiological knowledge into correlative SDMs. The reliability of future predictions is improved because this mechanistic knowledge encompasses the entire range of physiological response for the species, and thus, extrapolation is reduced. They can be used for detecting potential areas of extinction or invasion, assessing the potential effects of climate change on biodiversity (Pearson & Dawson, 2003) and guiding conservation actions. Despite all the limitations due to the inherent complexity of natural systems, Hybrid SDMs can be useful tools to assess the potential effects of climate change on biogeographic patterns.

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BIOSKETCH

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SUPPORTING INFORMATION

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