07/27/2021

Predicted Spatial Distribution of Corals in the Gulf of Mexico and the Caribbean

White Paper

July 2021

GULF OF MEXICO Fishery Management Council

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1.1 Background

Corals are animals, even though they may exhibit some of the characteristics of plants and are often mistaken for rocks. Hard corals, also known as scleractinian, and stony coral produce a rigid skeleton made of calcium carbonate ($CaCO_3$) in crystal form called aragonite. Colonial hard corals, consisting of hundreds to hundreds of thousands of individual polyps, are cemented together by the calcium carbonate 'skeletons' they secrete. Hard corals that form reefs are called hermatypic corals, and they are the primary reef builders in tropical regions. Although not reef-builders (i.e., ahermatypic), octocorals and smaller scleractinians are also important contributors to reef ecosystems. Soft corals are mostly colonial; what appears to be a single large organism is actually a colony of individual polyps combined to form a larger structure. Visually, soft coral colonies tend to resemble trees, bushes, fans, whips, and grasses. Coral reefs are diverse communities that provide habitat to many marine organisms. Losing these systems will affect many species that rely upon them and limit the benefits that they provide to the planet (Sheppard 2016; Dee et al. 2019; Gil-Agudelo et al. 2020; PJ and Riegl 2020). Although shallow-water coral reefs are not as abundant in the Gulf of Mexico (Gulf) as in other areas, such as the Caribbean, their uniqueness, isolated locations, and the rapid disappearance of certain species make their conservation highly important (Dee et al. 2019). Shallow and deep coral reefs are more widely distributed throughout the Gulf than previously thought, providing new avenues of research, but also new challenges for their sustainable management.

The Caribbean region has an estimated 26,000 km^2 of coral reef surface, which is about 7% of the world's shallow coral reefs (Burke and Maidens 2004). Reef development in the Gulf of Mexico is extremely limited due to the large inputs of sediment-laden freshwater from the North American continent. Shallow-water coral reefs in the Gulf occupy about 2,640 km^2 (<0.2% of Gulf) (Tunnell et al. 2007), whereas the extent of mesophotic corals, defined as light-dependent corals living at depths between 30–150 m (Hinderstein et al. 2010), is relatively low. About 85% of shallow-water corals in the Gulf are distributed along the coasts of Florida and Cuba (Tunnell et al. 2007), but the uniqueness and endemic nature of reefs throughout the Gulf make them particularly important. The coral coverage on reefs within the Gulf is also variable, having both some of the lowest in the Florida Keys, just above 10%, and the highest coral cover, almost 60%, in Flower Garden Banks and the Wider Caribbean Region (Gulf and Caribbean) (Schutte et al. 2010; Tunnell et al. 2007). Considering a better understanding of species geographic distributions is fundamental for designing and implementing management plans. Identifying the potential unknown distribution of the corals outside the Gulf would help the Council design an effective management strategy to protect the larval dispersion pathway for the long-term sustainability of the Gulf coral population.

Spatially explicit ecosystem models allow resource managers to better understand certain ecosystem processes; however, they require large amounts of data. One example of additional requirements is that these models require an initial spatial allocation of functional group biomass or abundance. It is not easy to develop biomass distribution grids, due to the lack of comprehensive stock assessment data (outside a handful of commercially valued species) and overall, there is limited spatially explicit distribution data from Gulf and Caribbean waters. In most cases, this limits the development of ecosystem models to those areas that are rich in fisheries independent data. While species distribution models (SDM's; Elith et al. 2006) are statistical tools that predict potential distribution into novel environmental space based on the observed relationship between environmental features and species occurrence (i.e., presence or absence), such models have been widely used to inform conservation and management planning (Lawler et al. 2011; Barrett et al. 2014). Though SDM’s are primarily developed for addressing issues other than climate change, there are studies available which base their conservation priorities on changes in the predicted distribution range of species occurrence from correlative SDMs under different climate scenarios (Carvalho et al. 2010; Triviño et al. 2013). Past studies on mapping Gulf coral distribution using SDMs mostly focused on deep water species (Georgian et al. 2014; Silva and MacDonald 2017; Etnoyer et al. 2018; Hu et al. 2020). Moreover, methods used to identify species distribution shifts range from mechanistic models (Hill et al. 2001) to climate-driven bioclimatic envelope-based (Walther et al. 2005), and correlative species distribution models (Peterson et al. 2011; Basher and Costello 2016). SDMs can provide insights into potential climate warming effects on species even when their physiological limitations are poorly known (Elith et al. 2010).

Rising ocean temperatures and global climatic changes are among the primary threats to coral reefs around the world and in the Gulf (Anthony et al. 2015). Coral bleaching has likely been one of the most important factors that have affected the wider Caribbean region corals over the last 30 years; with the 2005 bleaching was recorded as the most intense event of this type in the region. At some sites, it affected over 80% of shallow corals and killed 40% (Eakin et al. 2010). Also, as in many other parts of the world, overpopulation, coastal pollution, and overfishing are considered among the top anthropogenic stressors responsible for coral reef decline (Jackson et al. 2014). Given the threat faced by the shallow-water corals from anthropogenic and climatic factors, it is imperative to characterize the current distribution and range of corals in the Gulf before they are lost. Also, in order to understand how corals might respond to future climate warming, we ran SDM using a comprehensive set of distribution records of selected shallow-water corals from the Gulf and the surrounding region with environmental variables representing both present and future climate conditions. The aim of this document is to describe the methodology used for compiling environmental data, developing the species distribution models of selected Gulf and Caribbean coral species, and discuss the potentially suitable habitat to inform conservation and facilitate new discovery of coral reefs in the region.

2.1 Methods

2.1.1 Study Area

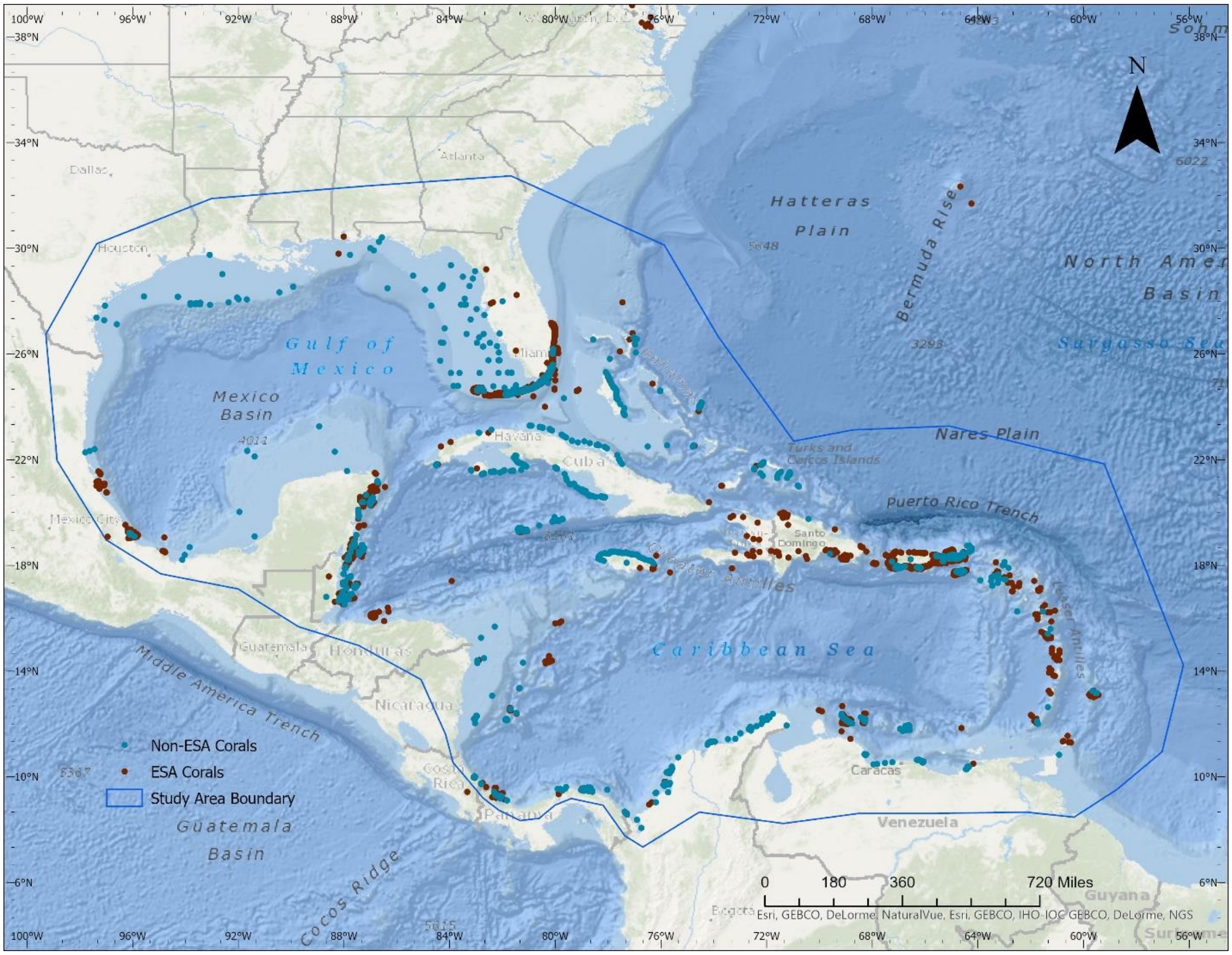

Figure 1. Gulf of Mexico Ecoregions study area with ESA and non-ESA coral occurrence records used for this study. Study area boundary in blue, brown dots represent the ESA-listed and green dot represent non-ESA listed coral observation records.

The study region includes the Gulf of Mexico Marine Ecoregions (Spalding et al. 2007) which includes the Gulf of Mexico basin and surrounding greater Caribbean regions (Figure 1). Considering the ocean is a continuous medium; corals could be recruited from any source population from the Caribbean to the Gulf. Therefore, instead of only limiting the model outputs for the Gulf, the study region for this study was expanded to include the Caribbean region to understand the overall present and future distribution of selected coral species in the regions. The Gulf of Mexico basin is roughly oval in shape and is approximately 810 nautical miles (1,500 km; 930 mi) wide. It is connected to the part of the Atlantic Ocean through the Florida Straits between the U.S. and Cuba, and with the Caribbean Sea via the Yucatán Channel between Mexico and Cuba. The Gulf is one of the world's 64 Large Marine Ecosystem and spans tropical and subtropical climate, and covered exclusive economic zones of the United States, Mexico, and Cuba (Sherman and Hempel 2009). The eastern Gulf encompasses the most developed coral reef formations. Meanwhile, the western Gulf is characterized by three types of banks. The south Texas Banks grow on relic carbonates, while the eastern banks off Texas and Louisiana have carbonate reef caps, and are either mid-shelf or shelf-edge/outer-shelf bedrocks (Rezak et al. 1990), with most of them offering habitat for mesophotic and deep-sea corals, but limited habitat for shallow corals and coral due to their depth. In the central Gulf, natural reefs (hardbottom areas) cover approximately 3.3% of its area; a small percentage that is limited by the large influence of discharges from the Mississippi River (Parker et al. 1983). However, thousands of decommissioned and active petroleum platforms serve as artificial reefs providing an important source of hard bottom habitat for the corals in the area (Sammarco et al. 2014; Schulze et al. 2020).

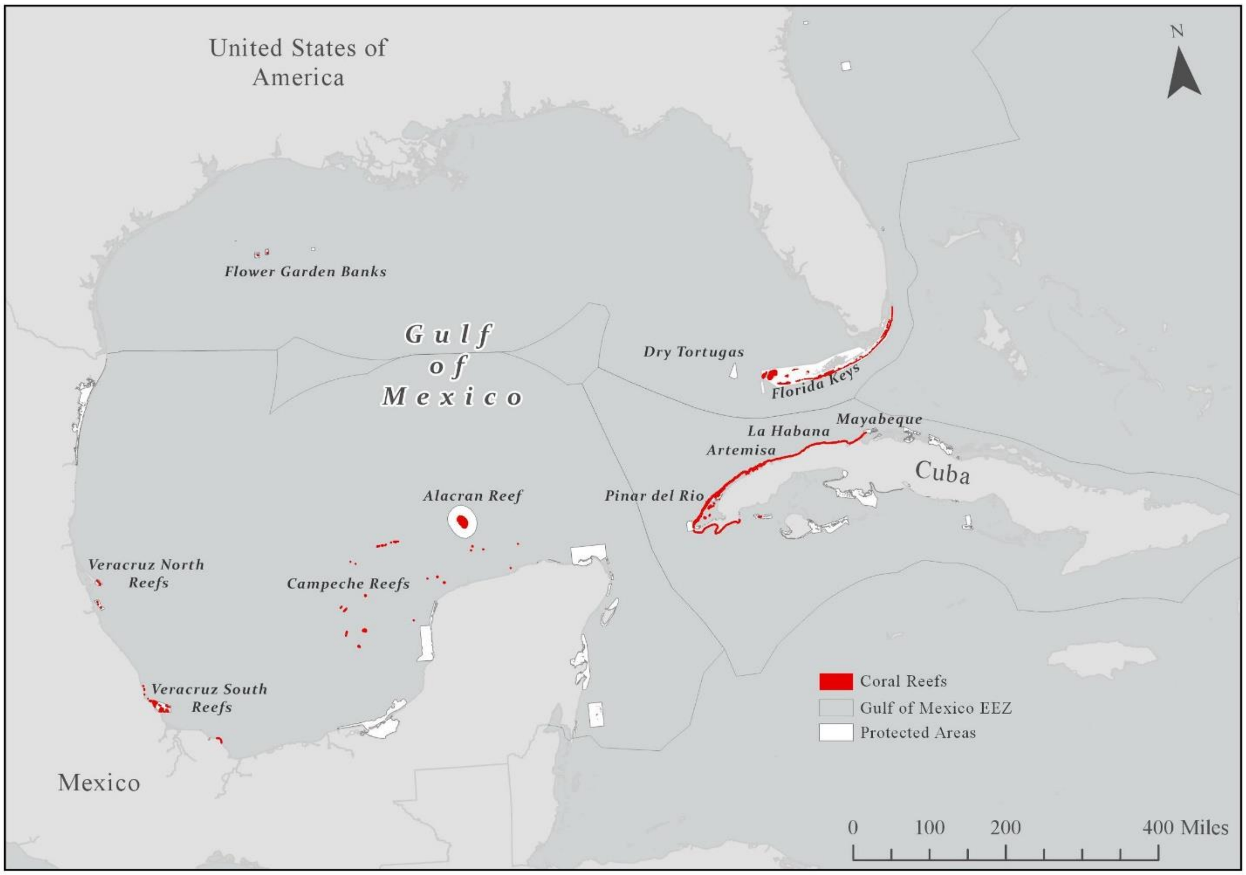

Figure 2. Coral reefs locations in the Gulf of Mexico from Gil-Agudelo et al. (2020)

The Gulf of Mexico has coral reefs located mostly in coastal mesophotic zones (up to ~150 m) around Texas, Louisiana, Florida, and Mexico. A wide array of deep-sea coral species (as well as other reef builders, such as sponges) are also found along the continental shelf and slope (Figure 2). The majority of these coral reefs are located within managed areas including Dry Tortugas National Park and Veracruzano Coral Reef System National Park, Flower Garden Banks and Florida Keys National Marine Sanctuaries, and Florida State Parks. Other coral reefs include Campeche Bank, Tuxpan, Tuxtlas, Yucatan Shelf, Florida Middle Grounds, and Pulley Ridge (Waddell and Clarke 2008; Ortiz-Lozano et al. 2013; Simmons et al. 2014; Dee et al. 2019).

2.1.2 Species Observation Data

A total of 19 coral species were selected for the study, which include seven threatened species under the U.S. Endangered Species Act (ESA) and 12 other common coral species (Table 1). The additional coral species were selected based on their ecological significance in supporting Gulf fishery habitats, the Florida Fish and Wildlife Conservation Commission's list of vulnerable coral species, and the availability of sufficient observational data from the Gulf to train the model. Coral observation data were compiled from the ESA coral database (available on the Coral Portal through the ESA coral explorer application) and other public biodiversity databases into a unified master dataset. A total of 85,854 observation records from year 2006 to 2018 of ESA coral species were obtained from ESA Coral Explorer (available at Coral Portal from ESA Coral Explorer). An additional 3,312 independent observation records were obtained from Ocean Biodiversity Information System (OBIS, 2020) for model validation. For other corals, 41,401 raw observation records were also obtained from OBIS which were summarized to 13,486 unique records at the final step after cleaning. All records were filtered to remove apparent geographic errors (i.e., coordinates plotting on land or in different regions) and duplicates, before combining them into a single dataset for model training or validation using ArcGIS.

Table 1. List of coral species used for this study. The column RecordsM indicated the number of individual observation records used for model development and the column RecordsV list the total number of records used for model's independent validation.

No	Common Name	Scientific Name	RecordsM	RecordsV	Data Sources
1	Elkhorn coral*	*Acropora palmata*	18504	516	1,2
2	Staghorn coral*	*Acropora cervicornis*	13086	520	1,2
3	Pillar coral*	*Dendrogyra cylindrus*	11019	173	1,2
4	Boulder star coral*	*Orbicella franksi*	10065	553	1,2
5	Mountainous star coral*	*Orbicella faveolata*	10535	741	1,2
6	Lobed star Coral*	*Orbicella annularis*	10859	720	1,2
7	Rough cactus coral*	*Mycetophyllia ferox*	10670	89	1,2
8	Lettuce coral	*Agaricia agaricites*	1232	-	2
9	Boulder brain coral	*Colpophyllia natans*	937	-	2
10	Elliptical star coral	*Dichocoenia stokesii*	746	-	2
11	Grooved brain coral	*Diploria labyrinthiformis*	911	-	2
12	Smooth flower coral	*Eusmilia fastigiata*	412	-	2
13	Maze coral	*Meandrina meandrites*	1062	-	2
14	Symmetrical brain coral	*Pseudodiploria strigosa*	2126	-	2
15	Knobby brain coral	*Pseudodiploria clivosa*	751	-	2
16	Great star coral	*Montastraea cavernosa*	1889	-	2
17	Massive starlet coral	*Siderastrea siderea*	2247	-	2
18	Smooth star coral	*Solenastrea bournoni*	130	-	2
19	Blushing star coral	*Stephanocoenia intersepta*	1043	-	2

* ESA corals; Sources: 1. ESA Coral Explorer, 2. Ocean Biodiversity Information System.

2.1.3 Environmental Data

Base environmental data were obtained from the Global Marine Environment Datasets (GMED)(Basher et al. 2014), namely depth, slope, temperature, salinity, bottom current, and primary productivity. These variables were selected in terms of their relevance to coral distribution based on a literature review and availability of relevant projected environmental layer for the future. Environmental data layers were cropped to the study region boundary first, then raw data were extracted into a high resolution georeferenced spatial point grid (1 km^2). Continuous raster surface of 1 km x 1 km resolution was interpolated using Inverse Distance Weight (IDW) method in ArcGIS and then used for developing the species distribution models (Figure 3). The 1 km^2 grid size was selected based on compatibility with other management data from the region (e.g., electronic logbook and vessel monitoring aggregation data).

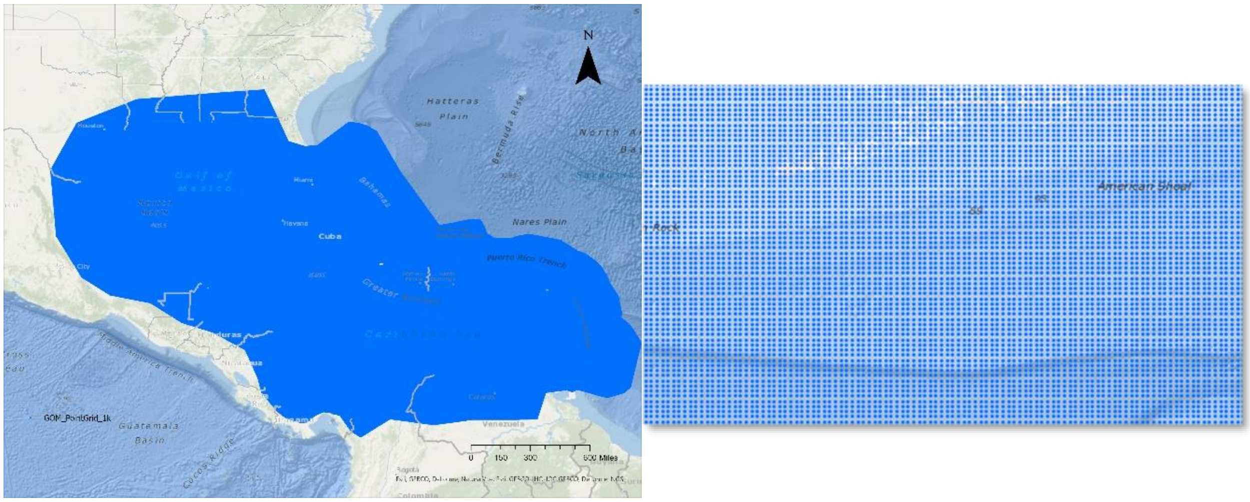

Figure 3. High resolution 1 km x 1 km point grid of Gulf Marine Ecoregions used in this study to extract and interpolate environmental data. Full LME with Grids (left), a zoomed version of the grid (right).

The variables were mostly derived from remotely sensed and in-situ measured datasets, and had a spatial resolution (pixel size) of 5 arc-min or ca. 9 km near the equator. Environmental data layers incorporating projected changes in climate were compiled from the Intergovernmental Panel for Climate Change (IPCC) high emission scenario (Representative Concentration Pathway; RCP 8.5) of Hadley Centre Global Environmental Model (HadGEM2-ES), based on Atmosphere Ocean Global Circulation Model (AOGCM). These projected environmental raster data grids of the year 2100 were integrated with the same present-day geospatial raster grid. As corals are benthic, we used environmental variables reflecting environment conditions near the seabed (e.g., in both Present and Future models). Overall the final dataset for present and future conditions was comprised of depth (depth, m), slope (slope, degree), sea bottom salinity (bSal, ppt), sea bottom temperature (SBT, ºC), sea bottom current (bCur, m/s) and primary productivity (Prod, mgC m^{-2}/day) (Figure 4) (Table 2).

Table 2. Descriptive statistics of used environmental data. All units are average annual mean, maximum and minimum for specific parameters.

Data Layers	Unit	Minimum	Maximum	Mean	Standard Deviation
Primary Productivity	mgC m-2/day	123.00	3015.00	448.33	300.02
Current	m/s	0.00	1.16	0.03	0.08
Salinity	PPT	23.15	37.04	35.17	0.81
Temperature	ºC	1.36	28.80	8.11	8.65
Slope	Degree	0.00	13.28	1.23	1.53
Depth	Meters	-8324.00	0.00	-2519.31	1890.88
Primary Productivity Year 2100	mgC m-2/day	111.00	3027.00	436.42	300.00
Current Year 2100	m/s	0.00	1.14	0.03	0.08
Salinity Year 2100	PPT	23.95	37.83	35.39	1.04
Temperature Year 2100	ºC	1.13	31.65	9.08	9.72

We used the Institut Pierre Simon Laplace (IPSL; http://icmc.ipsl.fr/) Future climate A2 scenario for the environmental data of the year 2100. Our scenario selection was limited to A2, as the deep-sea data layers in other climate scenarios were not available and generating them for this specific study by compiling raw data was beyond the scope of the study. The depth and slope in the future scenario were considered the same as the present depth since future predictions of bathymetry change were currently not available. All variables were derived from the mean annual average of in-situ or satellite data (See Basher et al. 2018 for details about all the layers). High correlations between environmental predictors may not only show spurious results, but negatively affect SDM performance and its transferability through space and time, as well (Heikkinen et al. 2006; Jiménez-Valverde and Lobo 2007; Liu et al. 2009; Dormann et al. 2013). None of the environmental variables used in our models showed strong correlations ($R^2 > 0.7$) when tested for pair-wise correlations using Pearson's correlation.

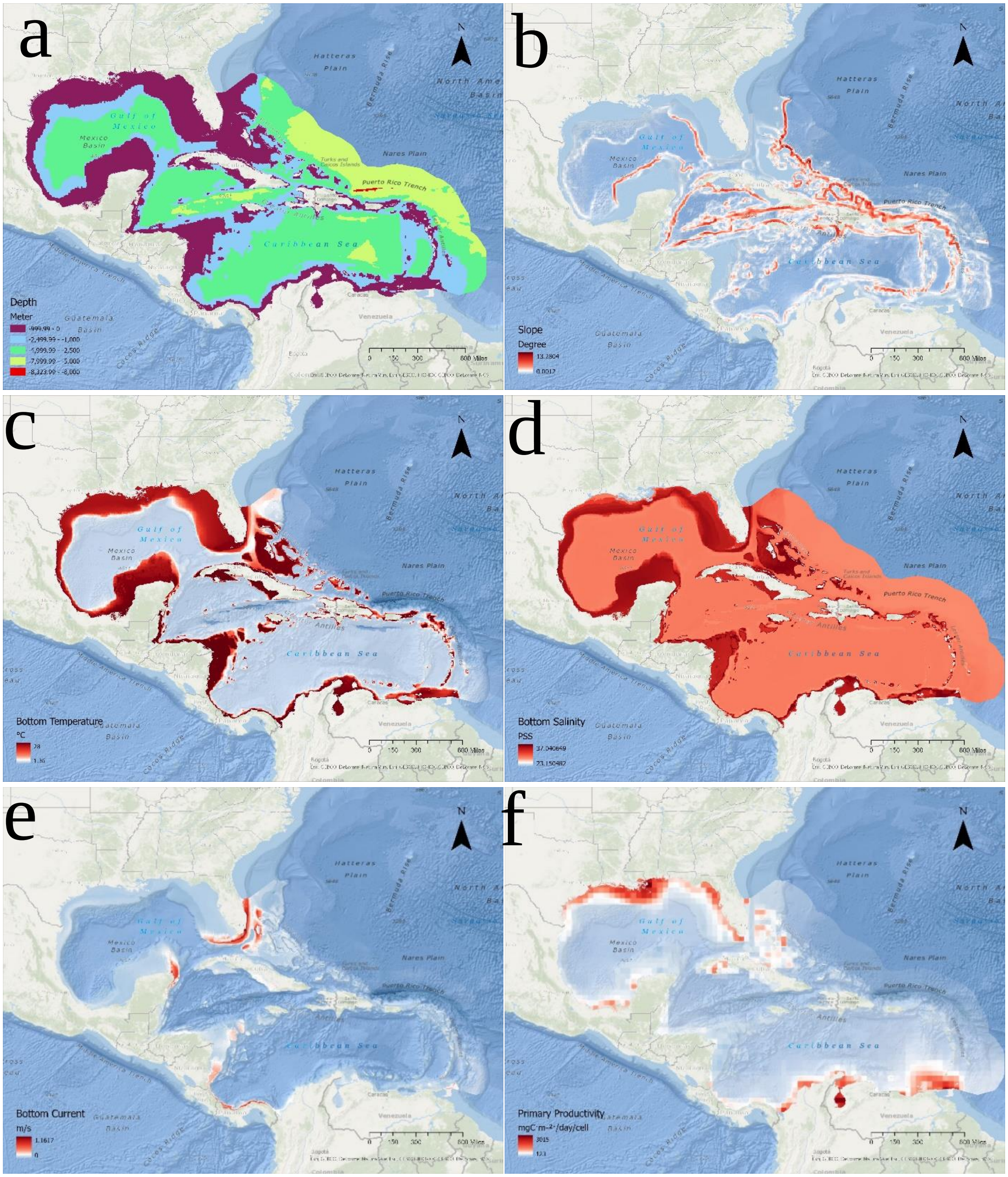

Figure 4. Environmental variables used for the SDM model development a) depth, b) slope, c) temperature, d) salinity, e) current, and f) primary productivity.

2.1.4 Model Building

MaxEnt 3.4.1 (Phillips et al. 2006) was used to model the current distribution of corals and to project Future distribution ranges. The program uses a machine-learning algorithm following the principles of maximum entropy (Jaynes 1982). Reviews comparing up to 16 models and of >200 taxa found that machine-learning methods, including MaxEnt, consistently outperformed traditional linear methods (Elith et al. 2006; Meißner et al. 2014) and that presence-only models were preferable because limited sampling can increase the prevalence of false absences within a dataset. MaxEnt starts with a uniform distribution during the modelling process and successively fits the model to the data (occurrence records and environmental variables). MaxEnt repeatedly tests the predictive capability of the model and improves by iteratively permuting and varying the input variables and features thereof. This is measured in the log likelihood or "model gain", which illustrates the discrepancy between the model identified distribution and the uniform distribution (Elith et al. 2011). MaxEnt thus specifies the relative suitability of the environment (interpreted as the potential geographic distribution) of the study organism.

MaxEnt models were generated using 10 bootstrap replicate runs with 10,000 random background points. The average of the 10 predictions across all replicates was used for further analysis. We excluded duplicate records that fell within individual pixels of background environment layers on each dataset using the `Remove duplicate presence records' feature in the MaxEnt software. The occurrence records were also split into 75% for training and 25% for testing for bootstrap replications. We set the maximum iterations to 1,000 to facilitate model convergence. As suggested by Phillips & Dudik (2008) the default regularization (i.e., smoothing) value was used, because it results in better performance of evaluation data for presence-only datasets. We minimized unreliable extrapolation into areas with environmental conditions that were not encountered during model training using the `fade by clamping' option of the software. Any predicted areas having the prediction value below the Minimum Presence Threshold (MPT) were considered unsuitable for the species.

Models were projected onto `Future' environmental datasets at the end of the iteration phase in a separate instance. As the final procedure, in ArcGIS 10 we calculated the species range shift maps using the method described in Basher & Costello (2016).

2.1.5 Model Evaluation

The logistic model output format gives a predicted suitability value ranging from 0 (unsuitable) to 1 (optimal) (Phillips and Dudík 2008). The final output raster was classified into four classes based on the range of predicted suitability value: HS (High Suitability, 0.75-Maximum); MS (Medium Suitability, 0.5- 0.75); LS (Low Suitability, MPT-0.5), and NS (Not suitable, Values below MPT). These classified raster files were used to interpret the suitability of coral habitat in the Gulf. MaxEnt allows for model evaluation by the Area Under the Receiver Operating Characteristic Curve (AUC) (Phillips et al. 2006). AUC is a threshold-independent measurement of model discrimination. An AUC value of 0.5 indicates model predictions are not better than random and AUC > 0.9 indicates high performance (Peterson et al. 2011). We used a random data split approach to evaluate model performance using a bootstrap procedure with an evaluation dataset (25% of the entire Present species distribution records were used for validation at random in each iteration of the model run).

We used percent variable contribution and jack-knife procedures in the software to investigate the relative importance of different environmental predictors. The jack-knife procedure produces a model by using variables in isolation to examine how well the result fits the known model gain (for both training and test data). Response curves were used to evaluate the relationships between environmental variables and the predicted presence probability of corals. Probability of presence values, which ranged from 0 to 1, where 0 meant no probability of presence and 1 meant the highest probability of presence at that particular location, were extracted from the average of all bootstrap models on each data set using the "Extract Values to Point" function of Spatial Analyst in ArcGIS.

Using an independent dataset is the optimal method for evaluating model performance (Phillips and Dudík 2008). We evaluated the ESA coral model accuracy only, using the independent data. As for non-ESA corals, no additional independent data were available for the validation. The evaluation determines how successfully the models predicted the species' potential distribution outside its given sampling locations.

3.1 Results

3.1.1 Predicted distributions

All the SDM had a high predictive power based on the values of AUC > 0.88 (AUC ± SD, ESA 0.875 ± 0.003; Non-ESA 0.930 ± 0.004) (Table 3). The minimum presence threshold (MPT) values were between 0.002 to 0.010 for ESA and 0.001 to 0.042 for Non-ESA models respectively (Table 3). Comparing the accuracy of the present-day models using independent records, the accuracy of an independent record plotting into areas with high predicted suitability varied from 33-64% (Table 3). However, all of the independent records used to validate the model were all plotted into areas having prediction value above MPT with low prevalence value, suggesting the high predictive performance of all the models (Table 3). The relative importance of the environmental variables to the SDM showed that temperature had the highest explanatory power 46-72% for all coral species in the present and future climate conditions (Table 4). The second and third most important variables were slope (10-33%) and current (3.5-27%) (Table 4).

3.1.1.1 Present Distribution

The predicted present distribution of corals showed both ESA and non-ESA coral species are widely distributed in the Gulf and Caribbean regions. With the highest distributions around the Florida Keys, west of Campeche escarpment, west of Yucatan channel and in the Caribbean region (Figure 3). The maximum predicted suitability value was above 0.9 (Table 3). Models predicted 0.5 - 17 % (depending on the species of corals) with an average of 7% of the area (Table 5) being highly suitable for corals in the study area. About 79% of the areas on average were found to have low suitability or were not a suitable environment for the development of coral reef. All of the independent validation records occurred in areas having a medium to a high probability of coral distribution (Figure 5).

3.1.1.2 Future Distribution

The SDM under the predicted future (the year 2100) climate conditions showed a significant contraction of coral distribution of all species in the Gulf. There was, although, an increase in suitable areas in the northern Gulf (Figure 4 and figures in Appendix Figure A1). The model predicted a contraction of a suitable environment for all corals in the future compared to the present (4.6% vs 7.2% of areas an average of the total) because more areas (57% vs 47% on average) identified as ‘not suitable’ environments for coral in the future (Table 5). The model predicted 0.1 – 15% (depending on species) with an average of an overall 4.6% of the area in the future having high suitability for coral reefs, which is little over half of the present-day suitable areas (Table 5). The potential change in the range predicted by the model showed range expansion in the northern and northwestern region of the Gulf and a range contraction around the southern Gulf and Caribbean region for most of the coral species (Figure 4 and figures in appendix).

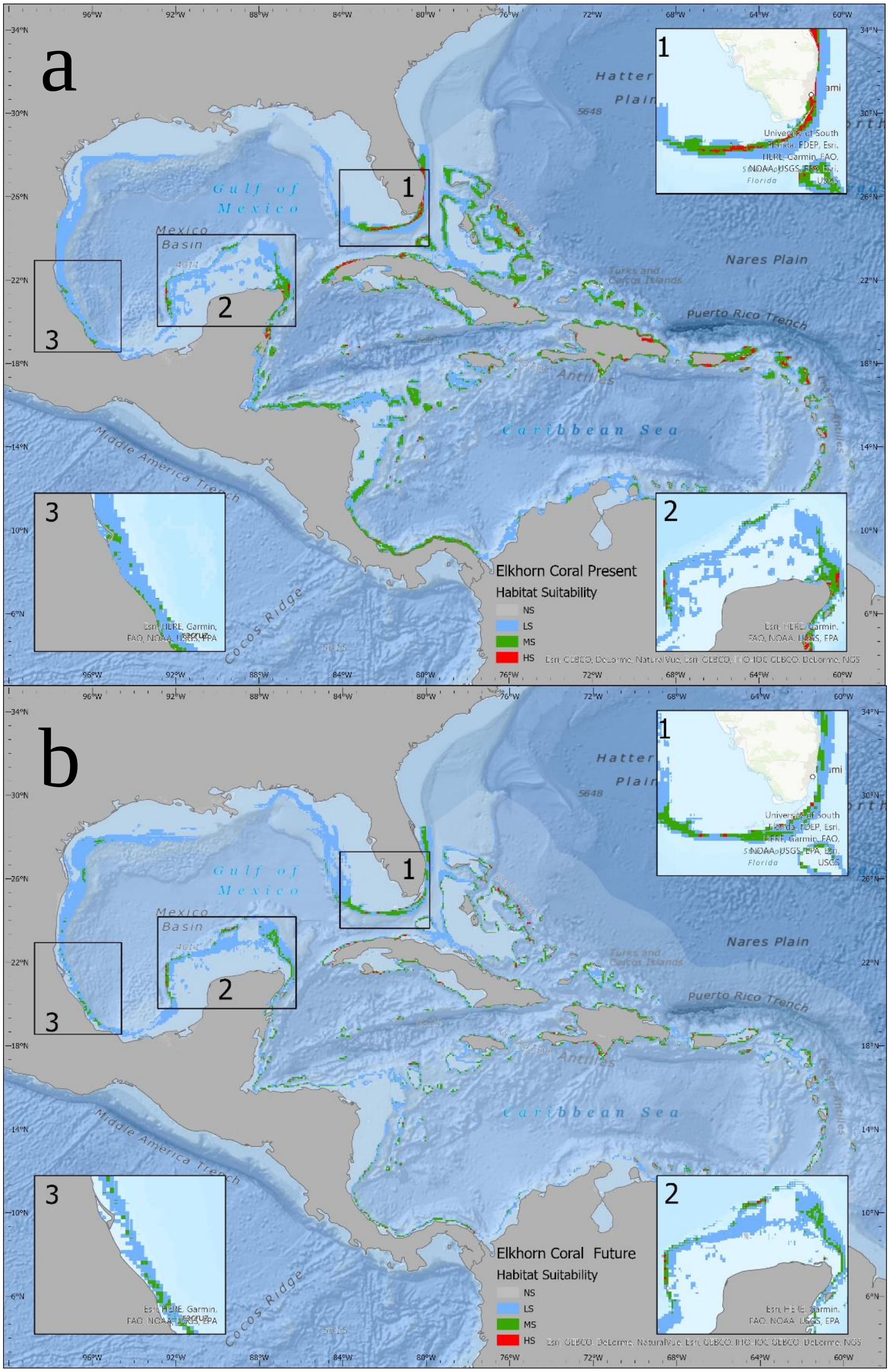

Figure 5. Predicted distribution of elkhorn coral during present (a) and future (b). Environment suitability: HS, High suitability (red); MS, Medium suitability (green); LS, Low suitability (light blue); NS, Not suitable (grey). See Appendix Figure A1 for maps of all other coral species. An online interactive version of the maps could be accessed from https://bit.ly/3sFf9s3

Among the ESA corals, boulder star coral, mountainous star coral, and lobed star coral will have more suitable habitat opened up around the southwestern Gulf. While for the non-ESA coral's, smooth star coral (*Solenastrea bournoni)*, massive starlet coral (*Siderastrea sidereal)*, great star coral (*Montastraea cavernosa)*, knobby brain coral (*Pseudodiploria clivosa*), and boulder brain (*Colpophyllia natans)* coral will have more suitable habitat areas around the southwestern Gulf, the Keys, and east coast of Florida. Almost all of these potential expanded suitable habitat areas are adjacent to existing respective coral populations. Thus, these areas would likely be colonized (Figure 4).

3.1.1.3 Change in Habitat

The results indicated an overall northward shift between the predicted distribution of present to future (the year 2100). The highly suitable present areas are located in the Keys, Caribbean, and areas close to the west of the Campeche bank region. A contraction of suitable habitat was predicted for most of the Caribbean, and Florida Keys sites (Figure 5). Sites in the north and southwestern Gulf would gain most of the expansion habitat where corals will gain suitable habitat in the future (Figure 6 and Appendix A2).

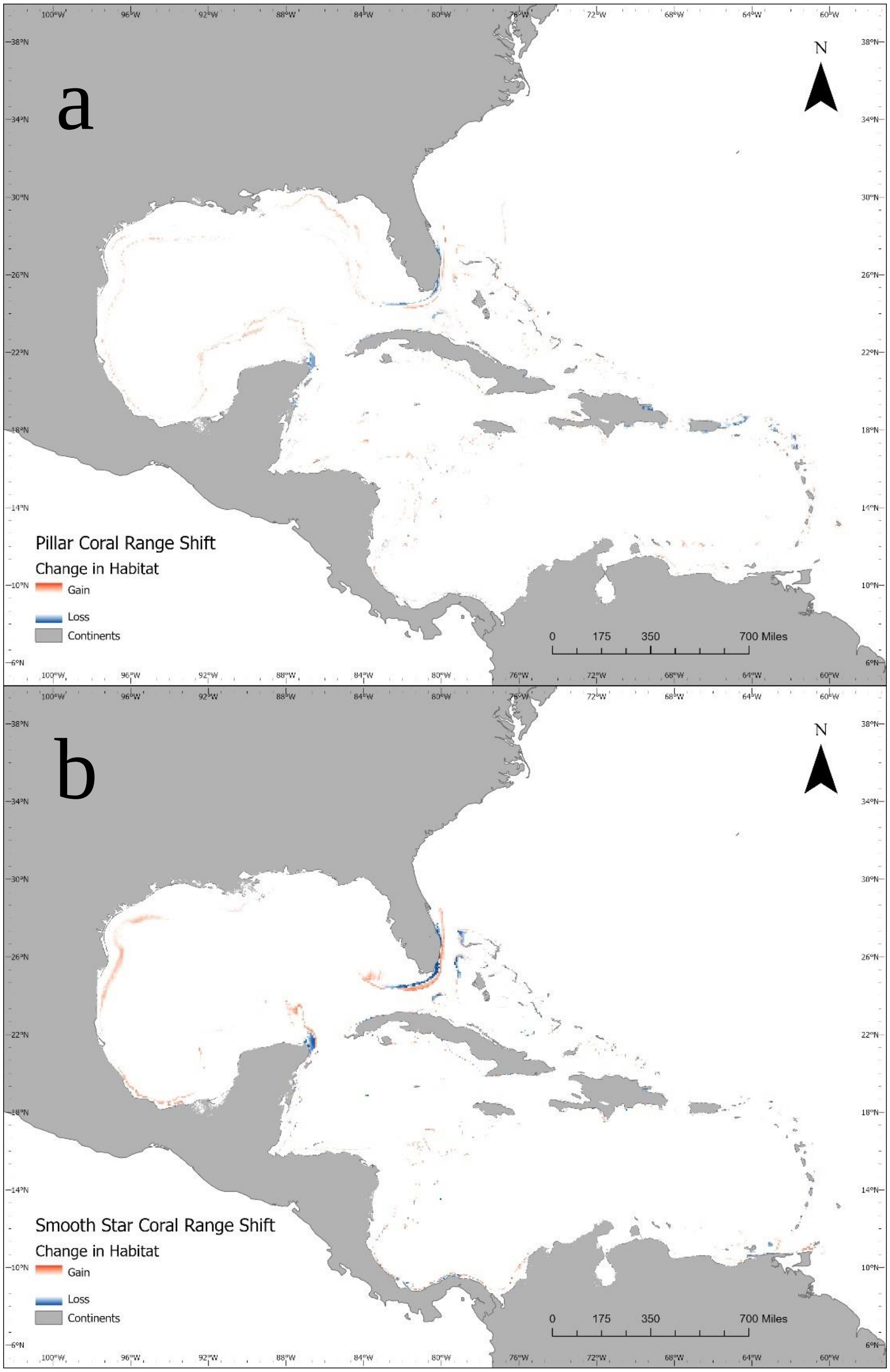

Figure 6. Changes in suitable habitat condition of pillar coral (*Dendrogyra cylindrus*) (a) and smooth star coral (*Solenastrea bournoni*) (b) based on predicted distribution of present and future. Areas that will become more suitable as habitat or where corals will gain habitat is marked as red, while areas where the habitat will be lost, or where coral habitats will contract, is marked as blue. See Appendix Figure A2 for change maps of all other coral species. An online interactive version of these maps could be accessed from https://bit.ly/3sFf9s3

Table 3. Summary of MaxEnt model results for all coral species. ‘Training gain’ indicates how closely the trained model is concentrated around the presence samples; for example, if the gain is 2, it means that the average likelihood of the presence samples is exp(2) ≈ 7.4 times higher than that of a random location, ‘Prevalence’ indicates average probability of presence in the sites outside the model training locations.

Model Summary	Training Samples #	Test Samples #	Training Gain	Test AUC	AUC Standard Deviation	Minimum Presence Threshold	Highest Probability of Presence	Prevalence	Ind. Validation Accuracy %
Acropora cervicornis	2741	900	1.18	0.884	0.003	0.45	0.91	0.19	64
Acropora palmata	2906	954	1.12	0.875	0.004	0.45	0.92	0.20	59
Dendrogyra cylindrus	2367	779	1.30	0.895	0.003	0.48	0.92	0.16	57
Mycetophyllia ferox	2295	755	1.33	0.902	0.003	0.48	0.92	0.16	46
Orbicella annularis	2778	910	1.15	0.878	0.004	0.45	0.94	0.19	59
Orbicella faveolata	2676	878	1.18	0.880	0.004	0.45	0.93	0.19	56
Orbicella franksi	2478	816	1.27	0.892	0.003	0.46	0.93	0.17	33
Agaricia agaricites	450	143	2.00	0.955	0.004	0.25	0.99	0.08	-
Colpophyllia natans	440	144	1.96	0.948	0.006	0.25	0.99	0.08	-
Dichocoenia stokesii	287	94	2.25	0.959	0.007	0.17	0.99	0.06	-
Diploria labyrinthiformis	444	144	2.02	0.953	0.005	0.28	0.99	0.08	-
Eusmilia fastigiata	189	60	2.29	0.960	0.006	0.24	0.99	0.06	-
Meandrina meandrites	407	133	2.14	0.961	0.004	0.24	0.99	0.07	-
Montastraea cavernosa	640	209	1.87	0.945	0.005	0.28	0.99	0.09	-
Pseudodiploria clivosa	337	110	2.24	0.965	0.004	0.22	0.99	0.06	-
Pseudodiploria strigosa	640	207	1.86	0.947	0.004	0.27	0.98	0.09	-
Siderastrea siderea	764	247	1.73	0.942	0.004	0.26	0.98	0.10	-
Solenastrea bournoni	79	25	2.81	0.971	0.011	0.16	1.00	0.03	-
Stephanocoenia intersepta	380	123	2.06	0.956	0.005	0.24	0.99	0.07	-

Table 4. Contribution of environmental variables in Coral Maxent Models development. Top 3 high values of `Contribution' and `Permutation Importance' are marked in bold. High values indicated they were the main predictors regulating the distribution of corals in the Gulf.

	Acropora cervicornis	*Acropora palmata*	*Dendrogyra cylindrus*	*Mycetophyllia ferox*	*Orbicella annularis*	*Orbicella faveolata*	*Orbicella franksi*	*Agaricia agaricites*	*Colpophyllia natans*	*Dichocoenia stokesii*	*Diploria labyrinthiformis*	*Eusmilia fastigiata*	*Meandrina meandrites*	*Montastraea cavernosa*	*Pseudodiploria clivosa*	*Pseudodiploria strigosa*	*Siderastrea siderea*	*Solenastrea bournoni*	*Stephanocoenia intersepta*
Predictor Influence																			
<u>Contribution %</u>																			
Depth	2.44	2.45	1.63	2.28	1.92	2.93	1.76	1.61	0.74	0.68	1.90	1.53	0.86	1.20	1.25	**1.87**	1.30	2.90	0.94
Slope	**14.37**	**15.30**	**14.78**	**14.46**	**15.68**	**15.18**	**15.06**	**29.01**	**28.86**	**33.62**	**27.87**	**27.23**	**30.13**	**28.40**	**24.84**	**30.42**	**24.70**	**9.21**	**25.82**
Current	4.24	4.38	4.20	3.69	3.42	4.28	3.87	1.11	**3.05**	1.38	**3.58**	**4.84**	**2.02**	**2.51**	**7.02**	1.44	**2.48**	**37.28**	**2.88**
Salinity	**6.39**	**5.01**	**5.99**	**6.30**	**5.61**	**5.06**	**5.26**	1.22	1.56	1.26	3.30	2.37	1.48	1.40	2.71	1.16	2.68	4.44	1.40
Temperature	**70.47**	**70.80**	**71.04**	**70.70**	**72.18**	**71.04**	**72.00**	**65.14**	**64.62**	**61.25**	**61.74**	**62.73**	**64.20**	**65.46**	**62.76**	**64.06**	**67.66**	**45.73**	**67.18**
Primary Production	2.09	2.06	2.36	2.57	1.19	1.51	2.05	1.90	1.16	**1.81**	1.62	1.30	1.32	1.04	1.42	1.06	1.18	0.43	1.78
<u>Permutation Importance</u>																			
Depth	0.37	0.64	0.42	0.39	0.29	0.39	0.34	**8.37**	3.80	**3.69**	2.95	**5.97**	**2.90**	2.41	**2.66**	**2.38**	**3.79**	0.90	**5.43**
Slope	**7.55**	**9.96**	**6.30**	**5.96**	**9.53**	**8.95**	**8.15**	**13.17**	**15.62**	**16.52**	**15.36**	**9.38**	**16.44**	**15.15**	**10.76**	**19.67**	**16.54**	**6.81**	**11.91**
Current	**4.75**	**5.47**	**4.83**	**5.08**	**4.20**	**3.41**	**3.71**	1.39	**3.36**	1.58	**3.71**	2.82	2.54	**2.78**	2.38	1.84	2.22	**6.25**	2.64
Salinity	1.55	1.33	1.42	1.77	1.22	1.31	1.23	0.99	0.69	0.86	0.45	1.40	1.52	0.72	0.47	0.45	0.57	1.32	2.03
Temperature	**82.95**	**80.30**	**83.87**	**83.30**	**82.21**	**83.64**	**83.74**	**74.31**	**74.02**	**75.84**	**75.21**	**79.55**	**74.65**	**76.98**	**82.06**	**74.54**	**74.98**	**84.47**	**76.38**
Primary Production	2.84	2.31	3.16	3.50	2.55	2.30	2.82	1.77	2.51	1.51	2.33	0.88	1.94	1.95	1.67	1.13	1.90	0.24	1.61

Table 5. Variation in area identified as 'highly suitable' environment for corals in Maxent model prediction. First two columns show the percentage of predicted highly suitable area out of total areas predicted to be suitable for coral habitat, and second two columns show the areas in million km2.

Coral Species	Percentage of total		Area in million km^2	
	Present	**Future**	**Present**	**Future**
Acropora cervicornis	0.67	0.30	0.19	0.10
Acropora palmata	0.65	0.26	0.23	0.09
Dendrogyra cylindrus	0.84	0.14	0.19	0.03
Mycetophyllia ferox	0.66	0.10	0.15	0.02
Orbicella annularis	0.58	0.22	0.27	0.08
Orbicella faveolata	0.63	0.37	0.27	0.13
Orbicella franksi	0.74	0.24	0.20	0.07
Agaricia agaricites	14.59	8.41	0.74	0.44
Colpophyllia natans	16.84	14.94	0.93	0.80
Dichocoenia stokesii	13.29	13.83	0.64	0.41
Diploria labyrinthiformis	1.23	0.30	0.92	0.23
Eusmilia fastigiata	16.12	5.73	0.76	0.19
Meandrina meandrites	12.69	10.16	0.58	0.39
Montastraea cavernosa	1.04	0.78	0.78	0.58
Pseudodiploria clivosa	14.28	12.41	0.61	0.54
Pseudodiploria strigosa	11.49	0.59	0.87	0.44
Siderastrea siderea	9.74	0.91	0.84	0.68
Solenastrea bournoni	9.94	7.83	0.36	0.33
Stephanocoenia intersepta	10.67	9.76	0.54	0.27

4.1 Discussion

Most of the coral reefs in the Gulf are reported to be in degraded condition, with the exception of Flower Garden Banks (a protected National Marine Sanctuary) in the northern Gulf, and Dry Tortugas National Park on the westernmost side of the Florida Keys (Waddell and Clarke 2008; Johnston et al. 2017; Dee et al. 2019). Models predicted suitable areas around the northern Gulf for most of the coral species at present, but the extent of suitable habitat areas seems to be increasing (Figure 4 and Appendix A1). This might be due to the projected overall 2º C temperature increase in the region in the year 2100 (Biasutti et al. 2012), making more areas habitable for the corals suitable in the Gulf than the present suitable areas, which are mostly located in tropics around the Keys and the Caribbean. This situation is opposite around the Florida Keys and Caribbean where most of the current habitats will be predicted to be lost in the future, potentially due to temperature range increasing above the threshold tolerance levels for the corals in these areas. Many studies in recent years identified elevated temperature as one of the reasons behind the loss of corals, thus is not surprising to find these habitats being lost due to increased temperature (Munday et al. 2008; Meissner et al. 2012; Spalding and Brown 2015; Graham et al. 2020).

The model suggests the geographic distribution of Gulf corals is mostly influenced by temperature, salinity, current, and slope. Reef-building corals grow optimally between 23° and 29°C and need a flowing water with optimal salinity and a rough substrate to attach. All these conditions are available in sloped areas in the ocean, indicating the model predicted the appropriate variables influencing the coral distributions. The result supports past studies that identified variations in water depth, currents, temperature, salinity, and turbidity play an important role in coral distribution and characterizing the biological communities in the northwest Gulf (Rezak et al. 1990; Schmahl et al. 2008). The result also agrees with the findings of other global studies which highlighted temperature, salinity, current, and intensity of light among the top factors influencing coral reef distributions in the ocean (Couce et al. 2012). This suggests these findings are more widely applicable for other coral species in the Gulf.

Species distribution models can predict the direction of species range contractions or expansions (Araújo et al. 2005; Basher and Costello 2016), but projections beyond the temporal range of a training dataset (i.e., distribution in the future) require a cautious interpretation to avoid potential pitfalls. When comparing the predicted suitable habitat for the present and future, most of the coral show a range expansion in the northern and western Gulf (Figure 6 and Appendix Figure A2). Range contraction is observed mostly around the equatorial regions where the projected temperature would be higher by the end of the century. However, some areas near the east of the Bahamas and Gulf of Honduras seem to have increased suitable habitats for the corals. These might be anomalies caused by the artifacts in environmental layers, but proper ground-truthing or additional observation data could ensure whether the identified areas have the potential to become suitable for coral growth in the future.

Furthermore, when compared the potential habitat range shift maps in relation to existing HAPCs in the Gulf, it seems north eastern Gulf HAPCs (i.e., Madison-Swanson, Edges, Steamboat lumps, and Florida Middle grounds) are already providing some protection to future coral expansion areas (Figure 7). Sites located in the northwestern Gulf might need additional management protection depending on the growth of coral cover over the coming decades. It might be necessary to set up monitoring programs for coral observation on selected northeastern and western sites to monitor whether coral reef habitats will increase on the predicted potential suitable habitat in the future. If an increase is observed, then the appropriate type of management measures would need to be implemented to protect the growing habitats in those regions.

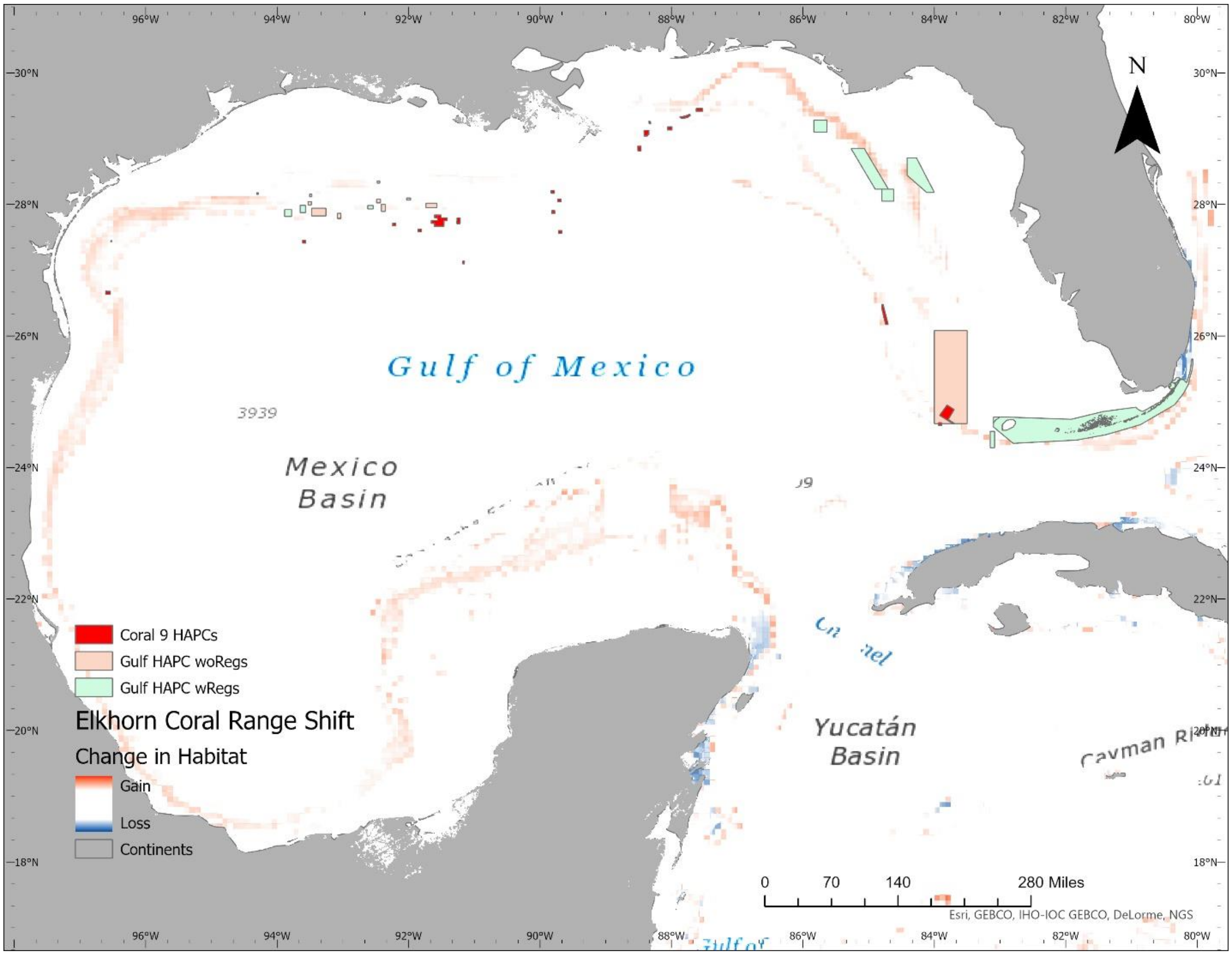

Figure 7. Elkhorn coral (Acropora palmata) predicted habitat change in relation to current HAPCs in the Gulf. Red indicates projected gain and blue indicates projected loss of habitat.

In general, when evaluating model performance, the AUC value tends to increase when the selected background model training area is larger than the species observed range. Although using AUC as the only method, model validation has its own caveats (Jiménez-Valverde and Lobo 2007; Lobo et al. 2010). It has been widely used in SDM studies for evaluating model performance (Lobo et al. 2010; Couce et al. 2012; Weinmann et al. 2013; Hu et al. 2020). All the models have relatively high AUC values (above 0.888) indicating the high performance of the models on identifying potentially suitable areas for the corals.

It should be noted the models were built on selected environmental layers due to the constraint of having similar data layer with the future projections. Although model development was tested with few other very relevant environmental data layers (i.e., euphotic layer depth, nutrients, pH, and rugosity), contribution of these variables to coral species distribution were minimal when they were included in the initial model runs compared to included variables. Due to their lower contribution they were not included in the final model development. As new data layers become available, the model could be updated to re-evaluate their contribution for the coral distributions.

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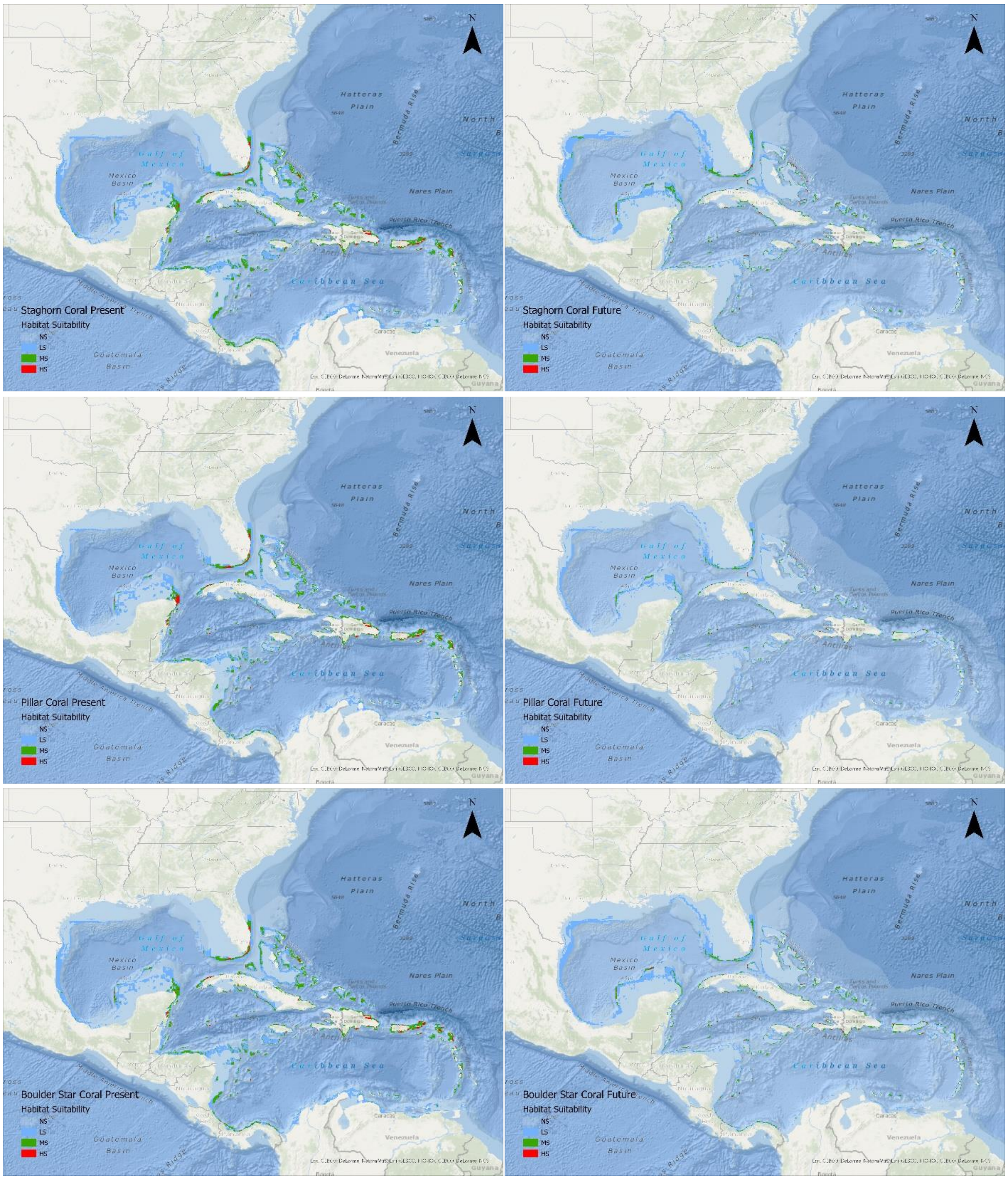
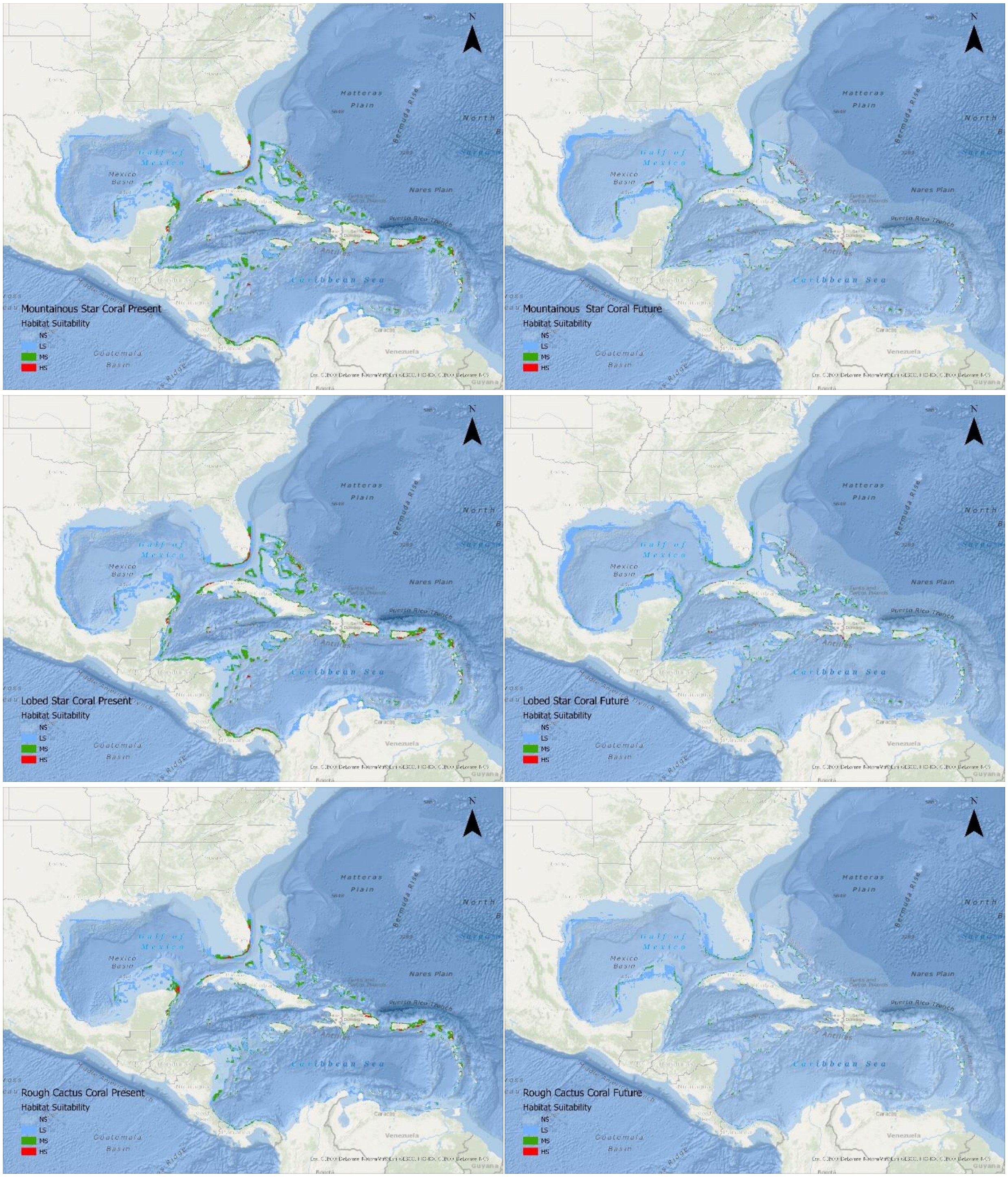
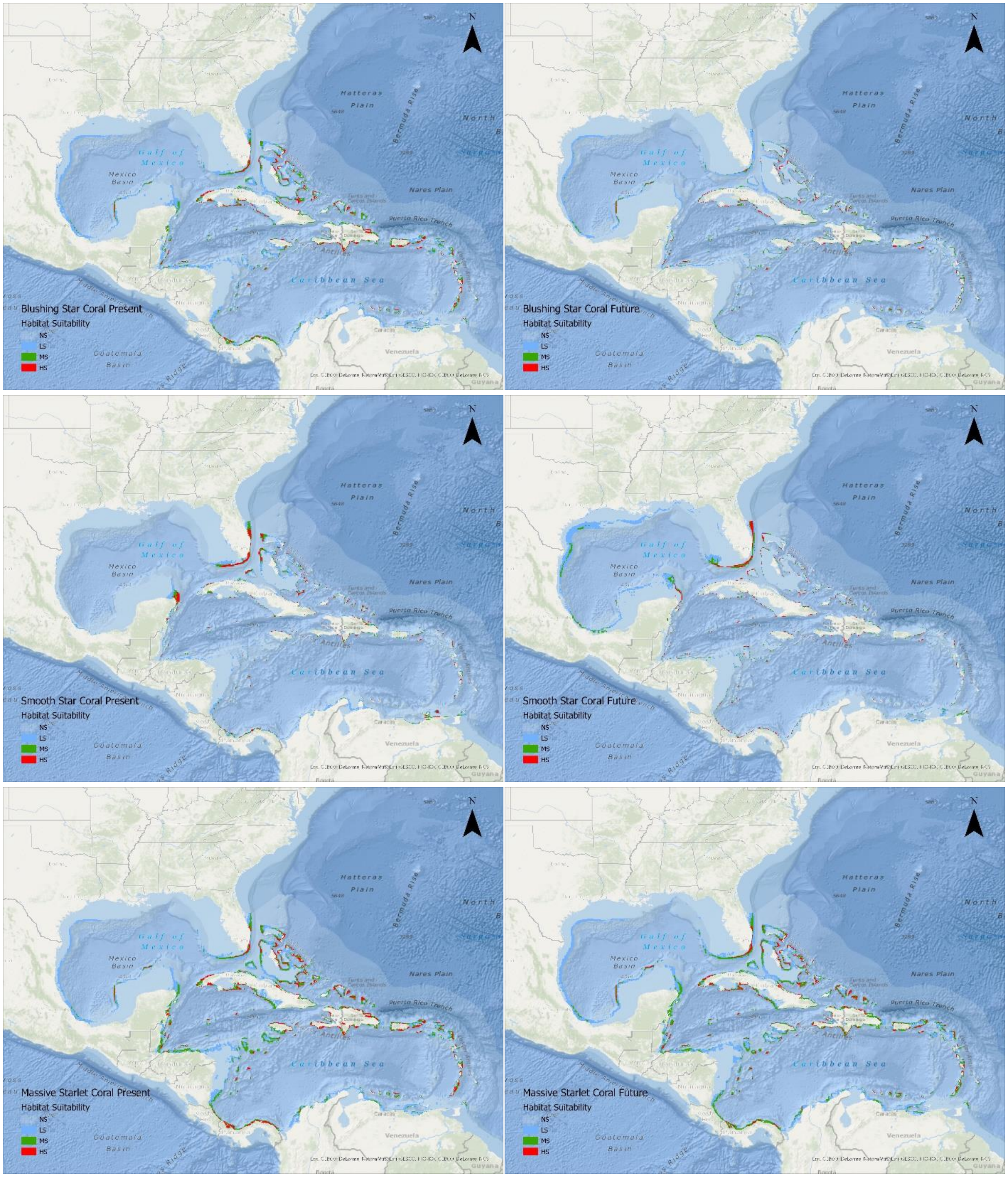
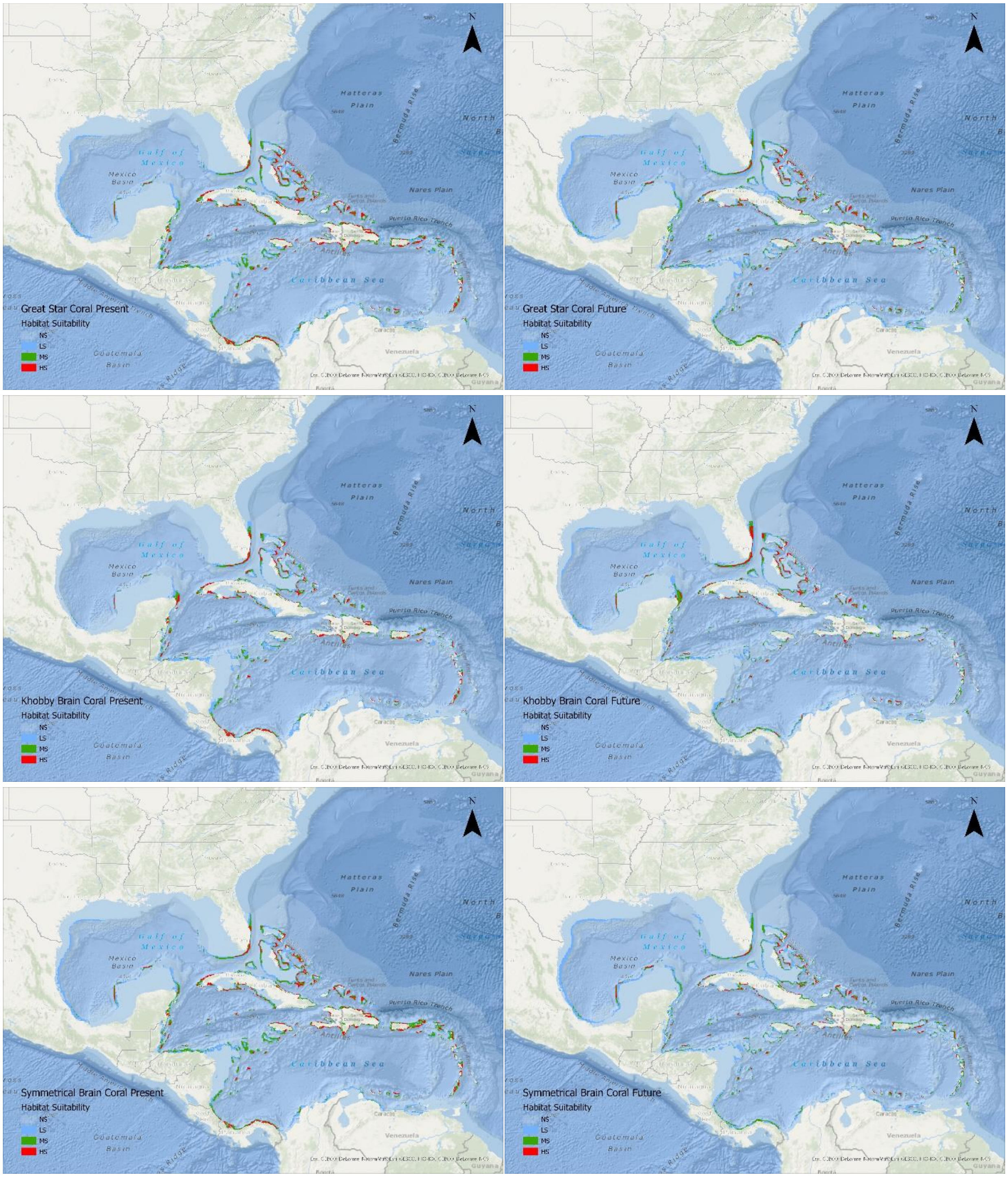
Appendix

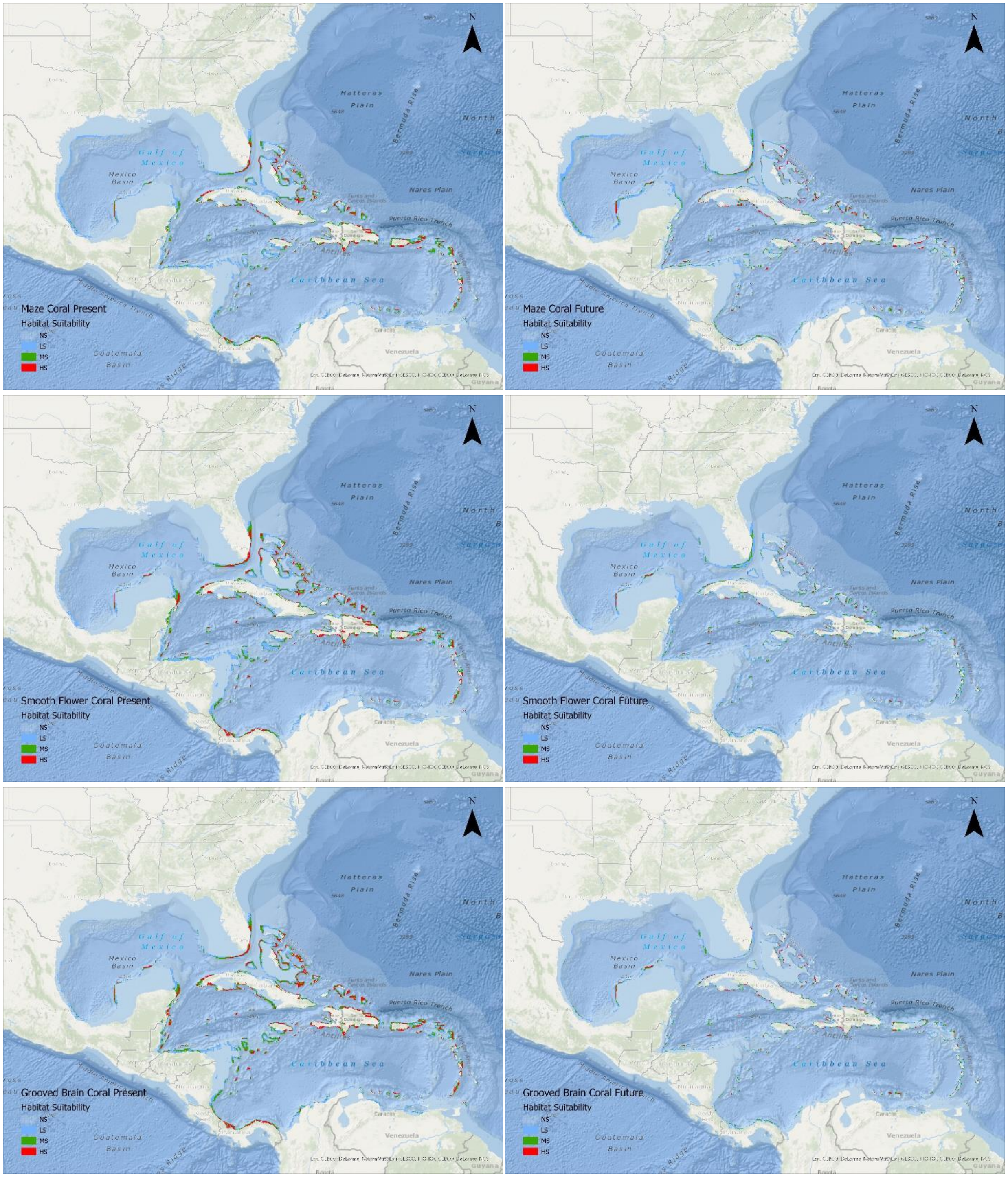
Figures A1: Predicted distribution of Gulf Corals during present and future. Environment suitability: HS, High suitability (red); MS, Medium suitability (green); LS, Low suitability (sky); NS, Not suitable (white). An online interactive version of the models could be accessed from https://bit.ly/3sFf9s3

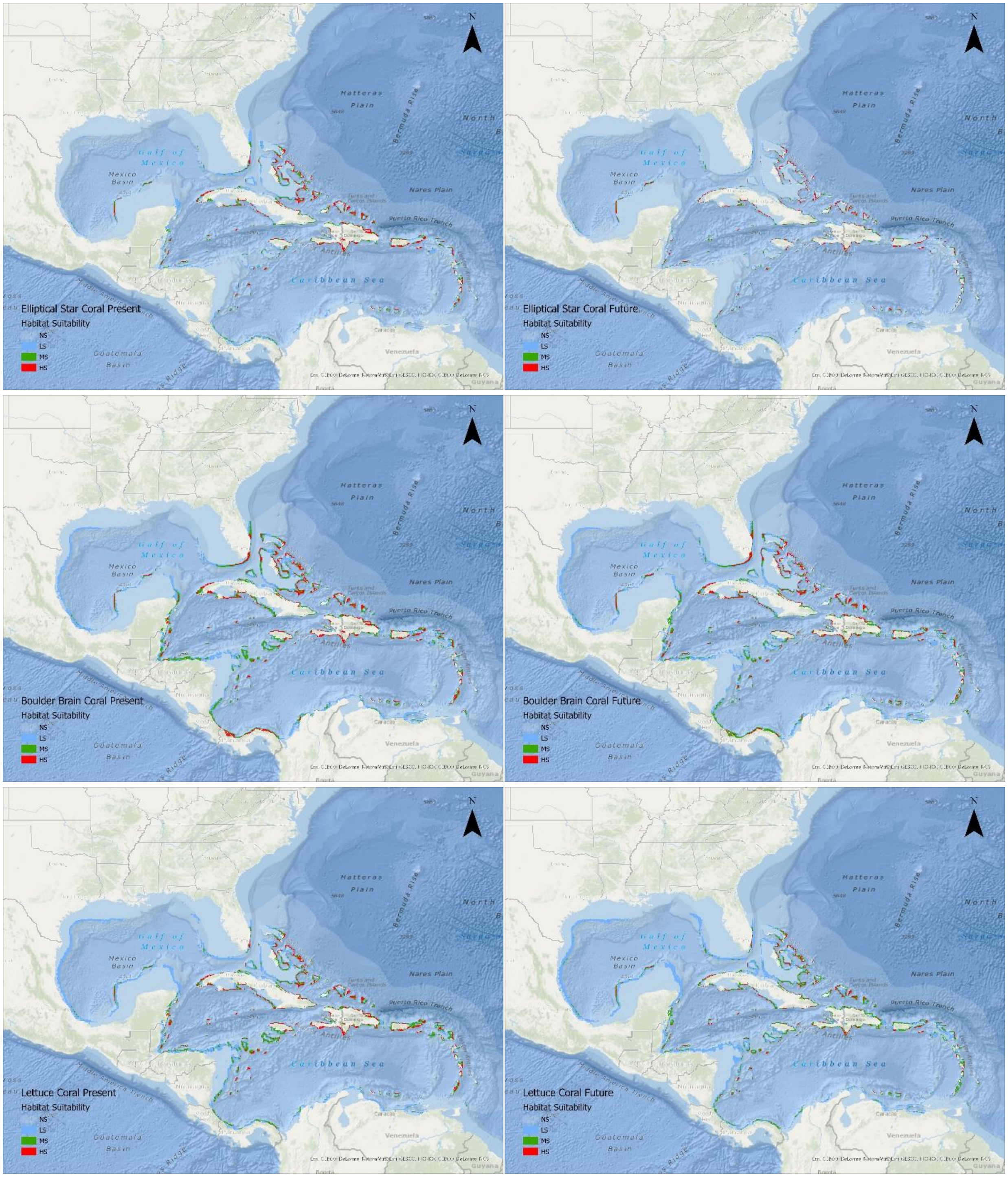



Mountainous Star Coral Present
Habitat Suitability
NS
LS
MS
HS
Mountainous Star Coral Future
Habitat Suitability
NS
LS
MS
HS
Lobed Star Coral Present
Habitat Suitability
NS
LS
MS
HS
Lobed Star Coral Future
Habitat Suitability
NS
LS
MS
HS
Rough Cactus Coral Present
Habitat Suitability
NS
LS
MS
HS
Rough Cactus Coral Future
Habitat Suitability
NS
LS
MS
HS
N
Hatteras Plain
Nares Plain
Gulf of Mexico
Mexico Basin
Caribbean Sea
Venezuela
Guatemala Basin

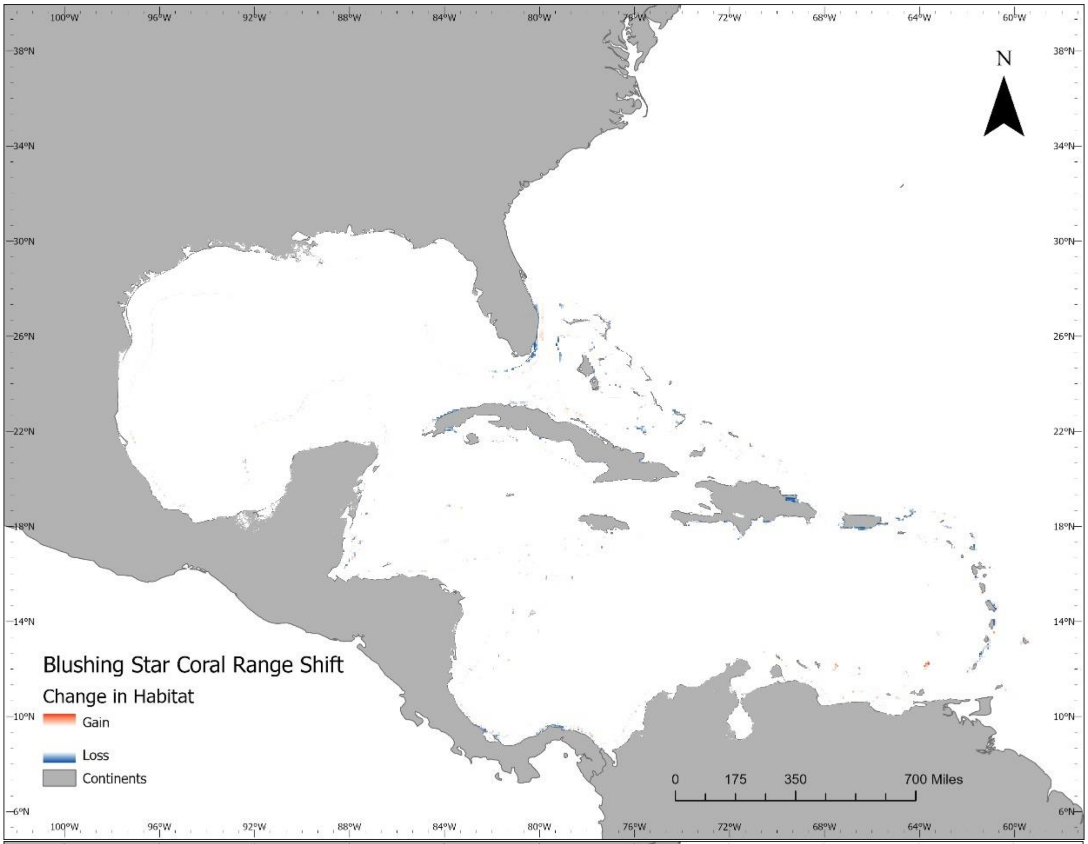

Blushing Star Coral Present
Habitat Suitability
NS
LS
MS
HS
Blushing Star Coral Future
Habitat Suitability
NS
LS
MS
HS
Smooth Star Coral Present
Habitat Suitability
NS
LS
MS
HS
Smooth Star Coral Future
Habitat Suitability
NS
LS
MS
HS
Massive Starlet Coral Present
Habitat Suitability
NS
LS
MS
HS
Massive Starlet Coral Future
Habitat Suitability
NS
LS
MS
HS
Gulf of Mexico
Caribbean Sea
Hatteras Plain
Nares Plain
Venezuela

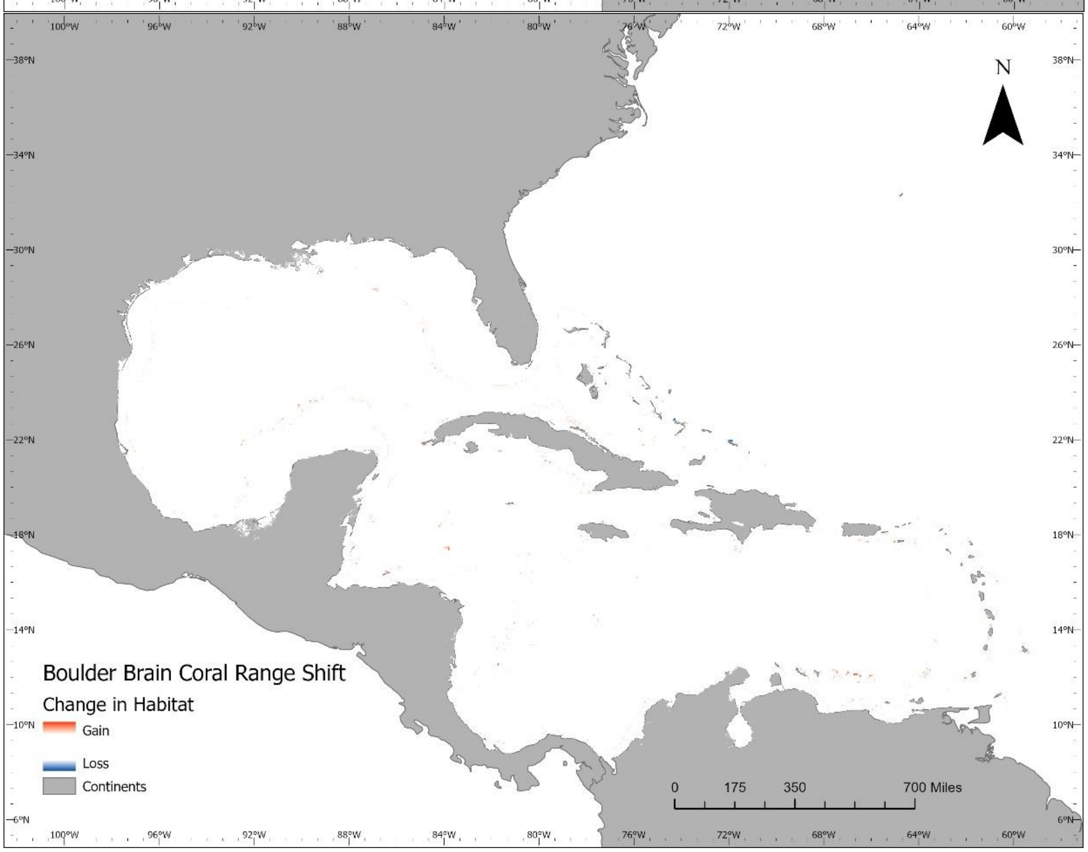

Great Star Coral Present
Habitat Suitability
NS
LS
MS
HS
Great Star Coral Future
Habitat Suitability
NS
LS
MS
HS
Khobby Brain Coral Present
Habitat Suitability
NS
LS
MS
HS
Khobby Brain Coral Future
Habitat Suitability
NS
LS
MS
HS
Symmetrical Brain Coral Present
Habitat Suitability
NS
LS
MS
HS
Symmetrical Brain Coral Future
Habitat Suitability
NS
LS
MS
HS

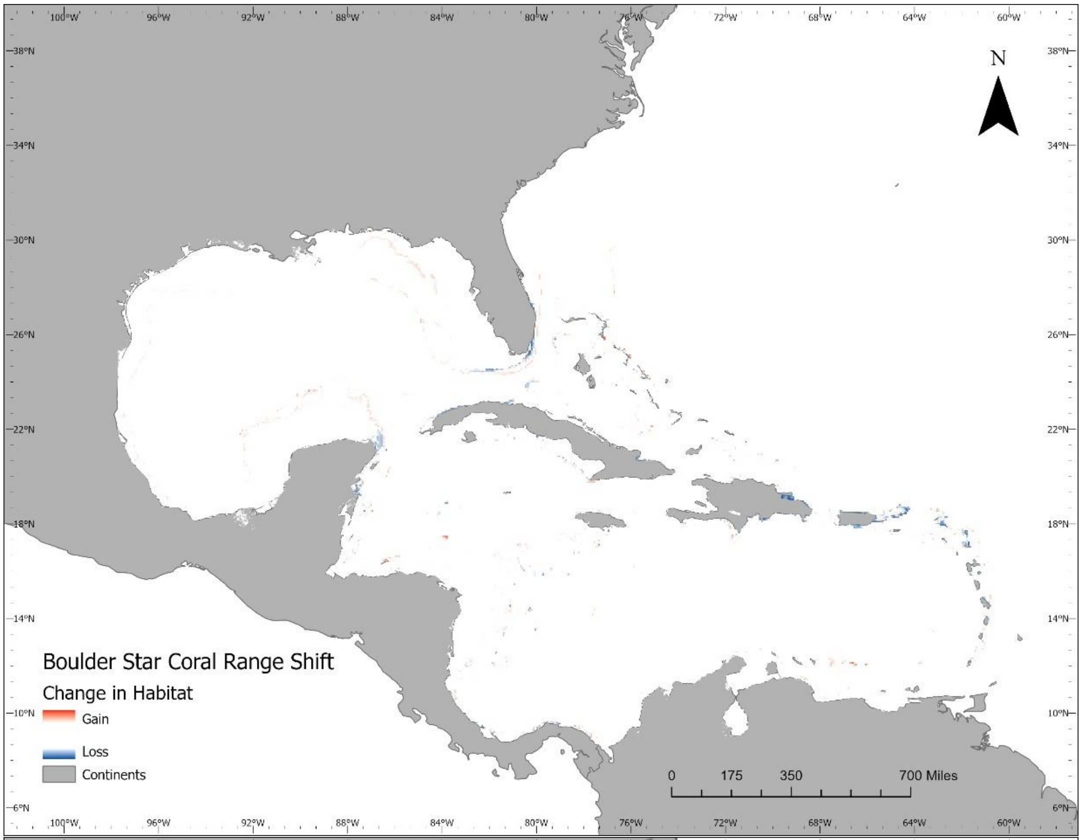

Maze Coral Present
Habitat Suitability
NS
LS
MS
HS
Maze Coral Future
Habitat Suitability
NS
LS
MS
HS
Smooth Flower Coral Present
Habitat Suitability
NS
LS
MS
HS
Smooth Flower Coral Future
Habitat Suitability
NS
LS
MS
HS
Grooved Brain Coral Present
Habitat Suitability
NS
LS
MS
HS
Grooved Brain Coral Future
Habitat Suitability
NS
LS
MS
HS
Gulf of Mexico
Caribbean Sea
Hatteras Plain
Nares Plain
Puerto Rico Trench
Venezuela

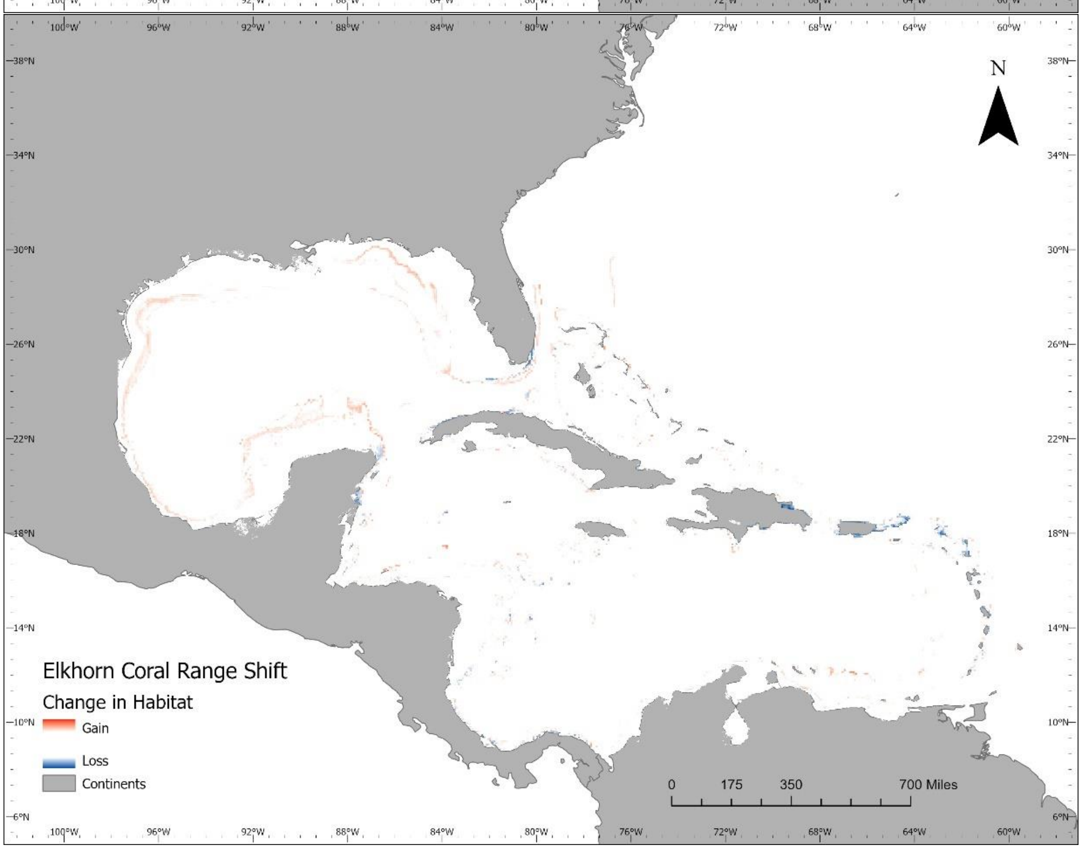


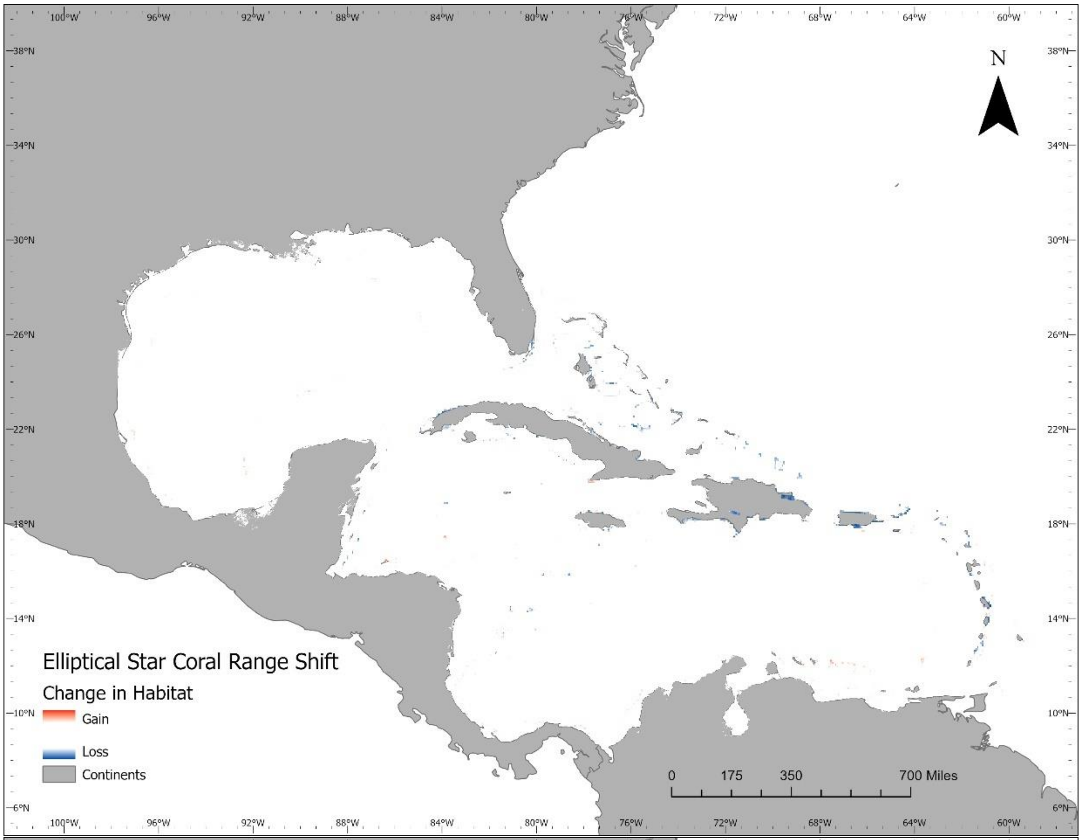
Figures A2: Changes in suitable habitat condition Gulf corals based on predicted distribution of present and future. Areas which will become more suitable habitat or where corals will gain habitat is marked as red while areas where the habitat will be lost or where coral habitats will contract is marked as blue. An online interactive version of these figures could be accessed from https://bit.ly/3sFf9s3

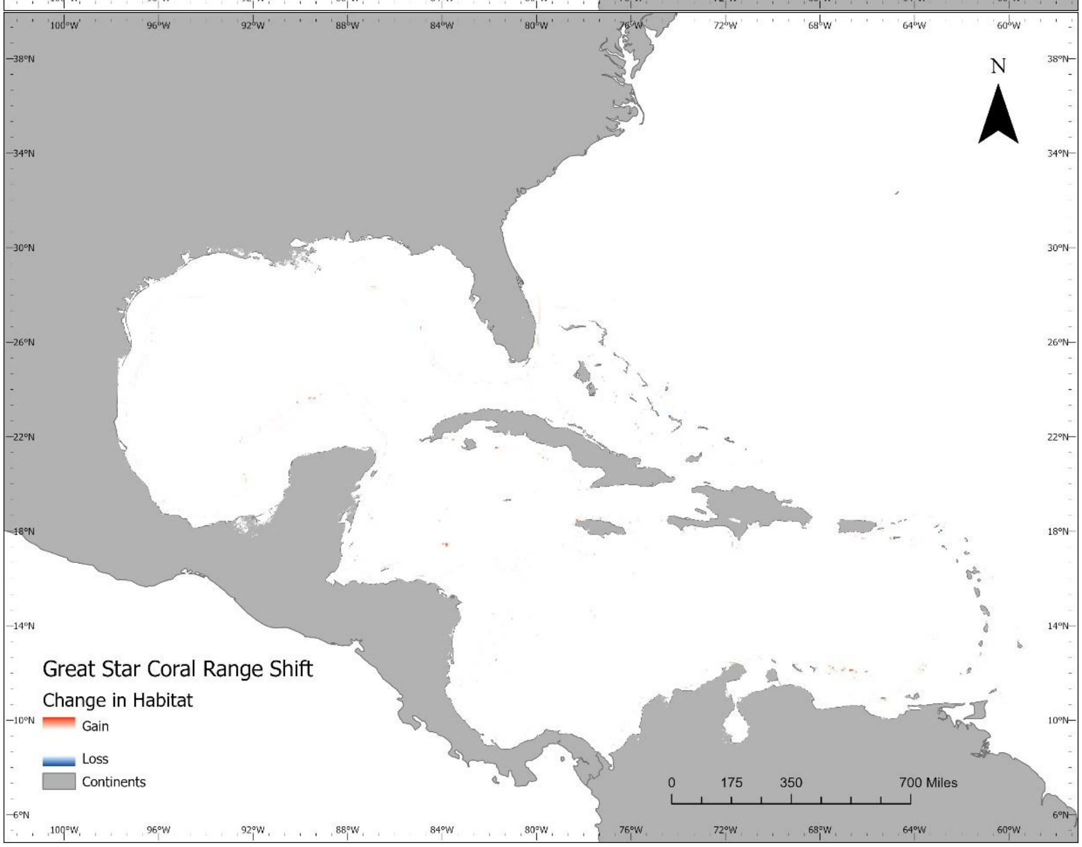

Blushing Star Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

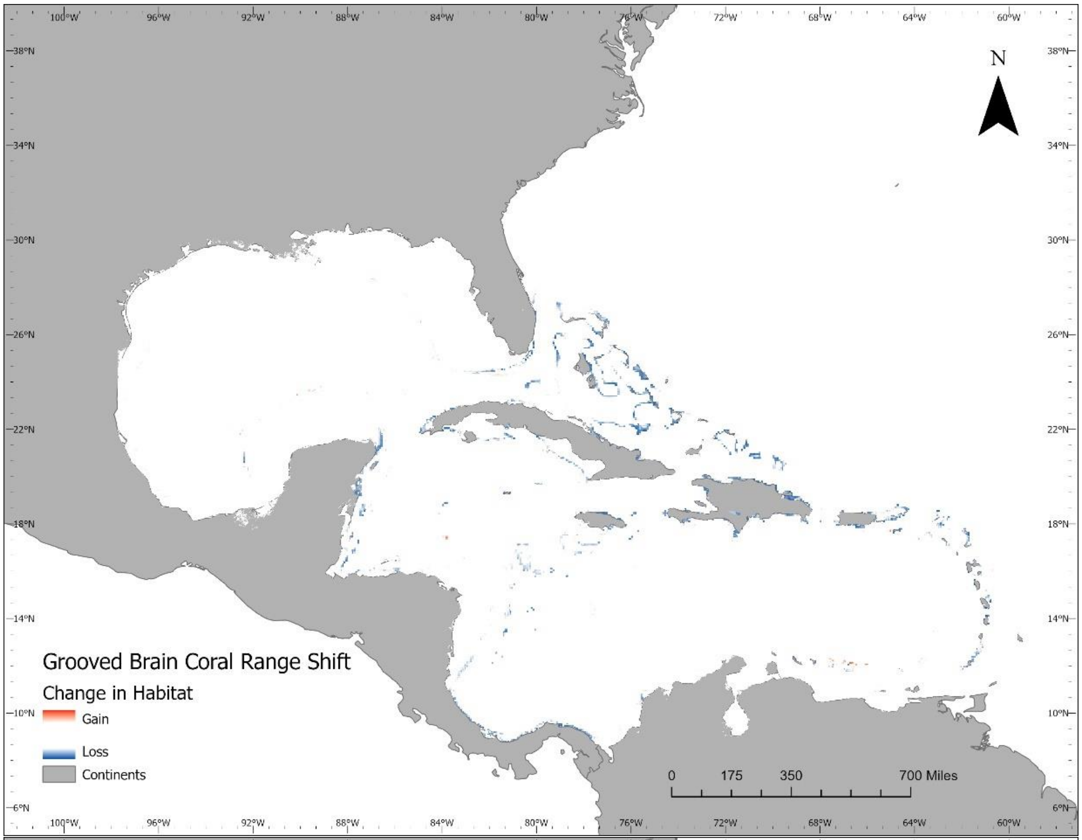

Boulder Brain Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

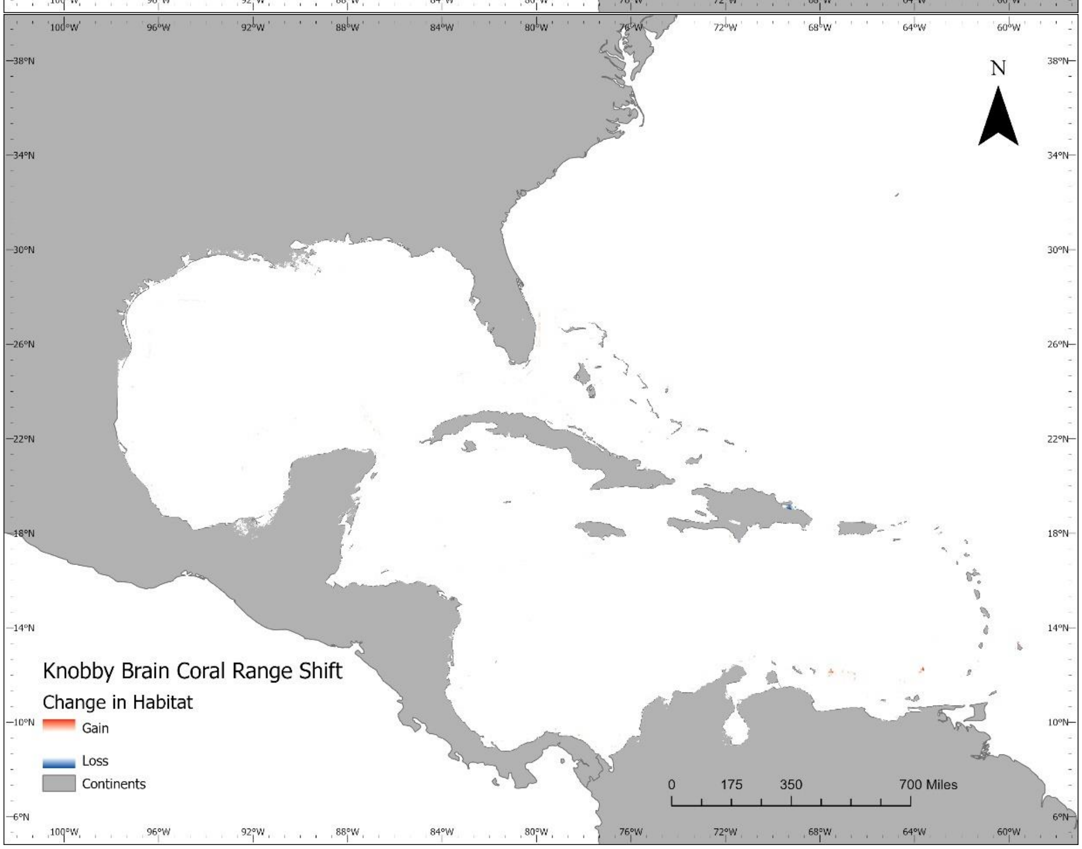

Boulder Star Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

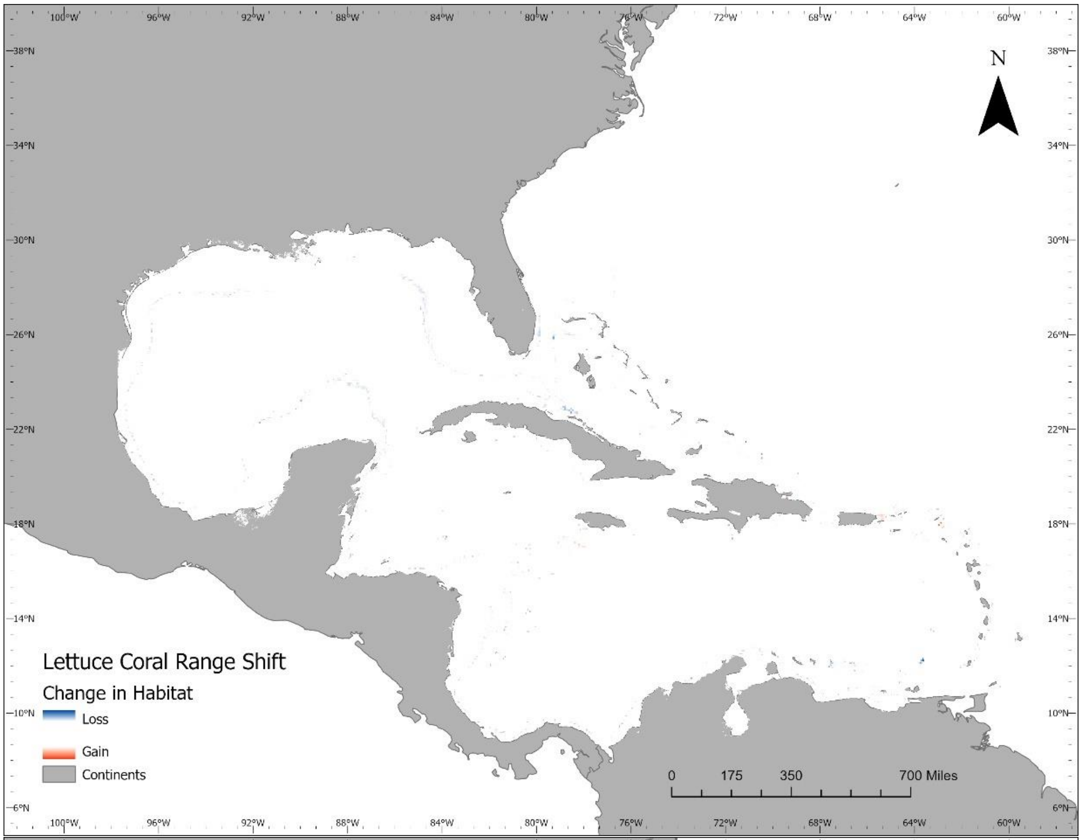

Elkhorn Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

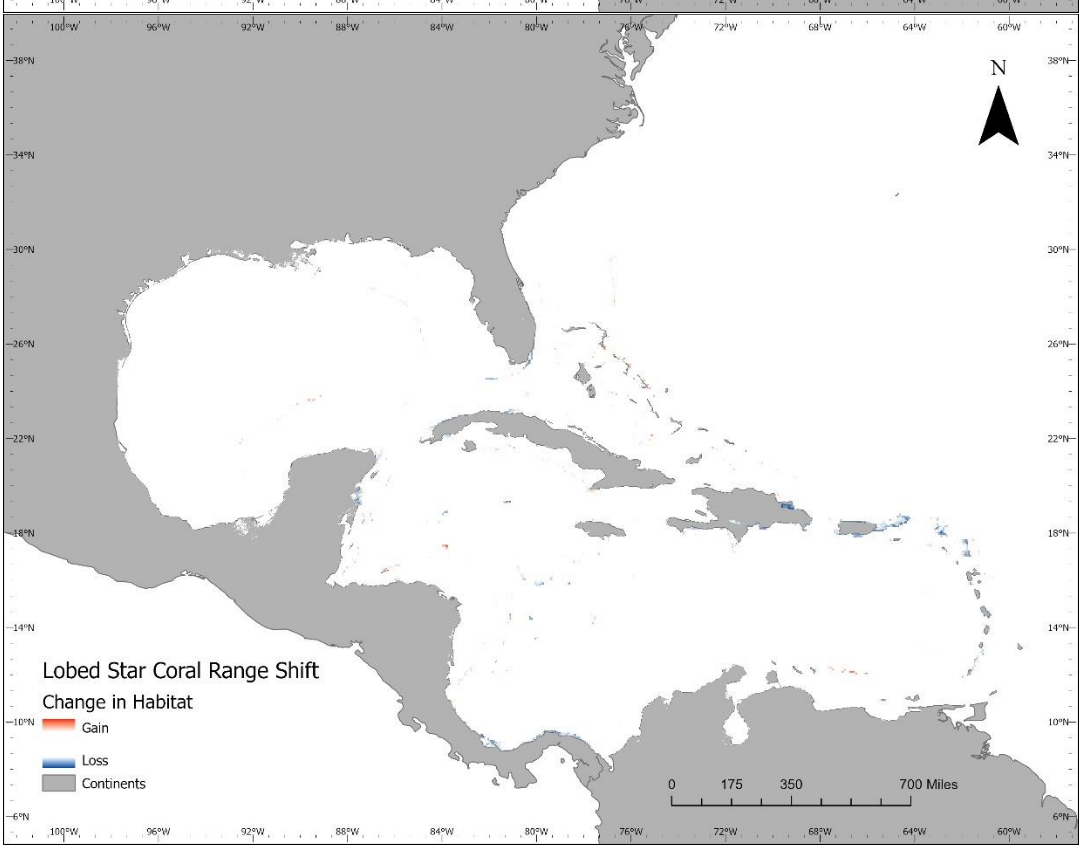

N
Elliptical Star Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles

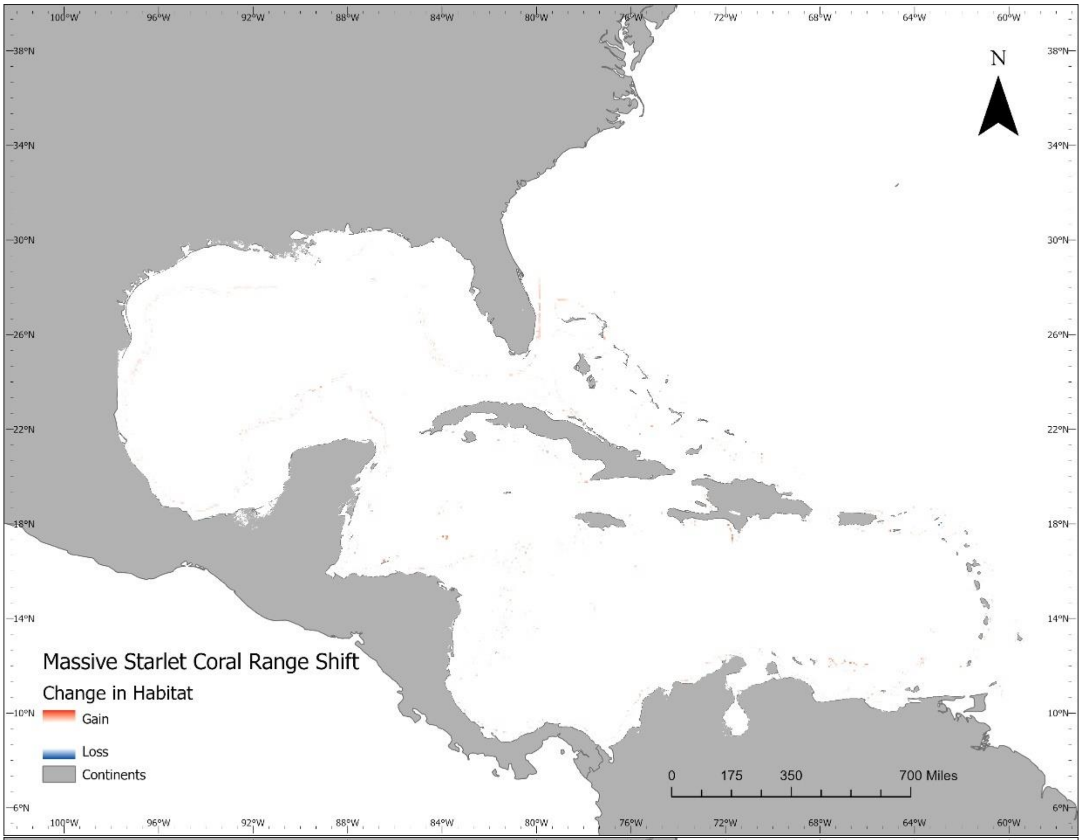

N
Great Star Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles

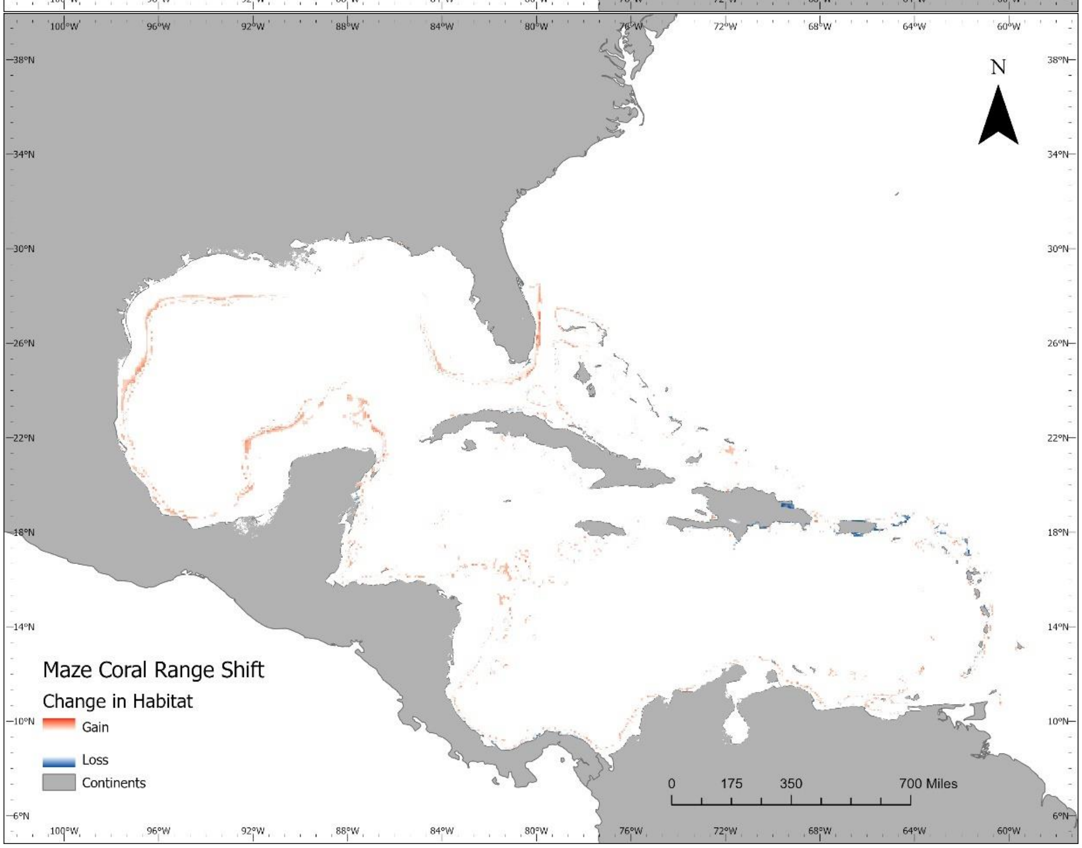

Grooved Brain Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

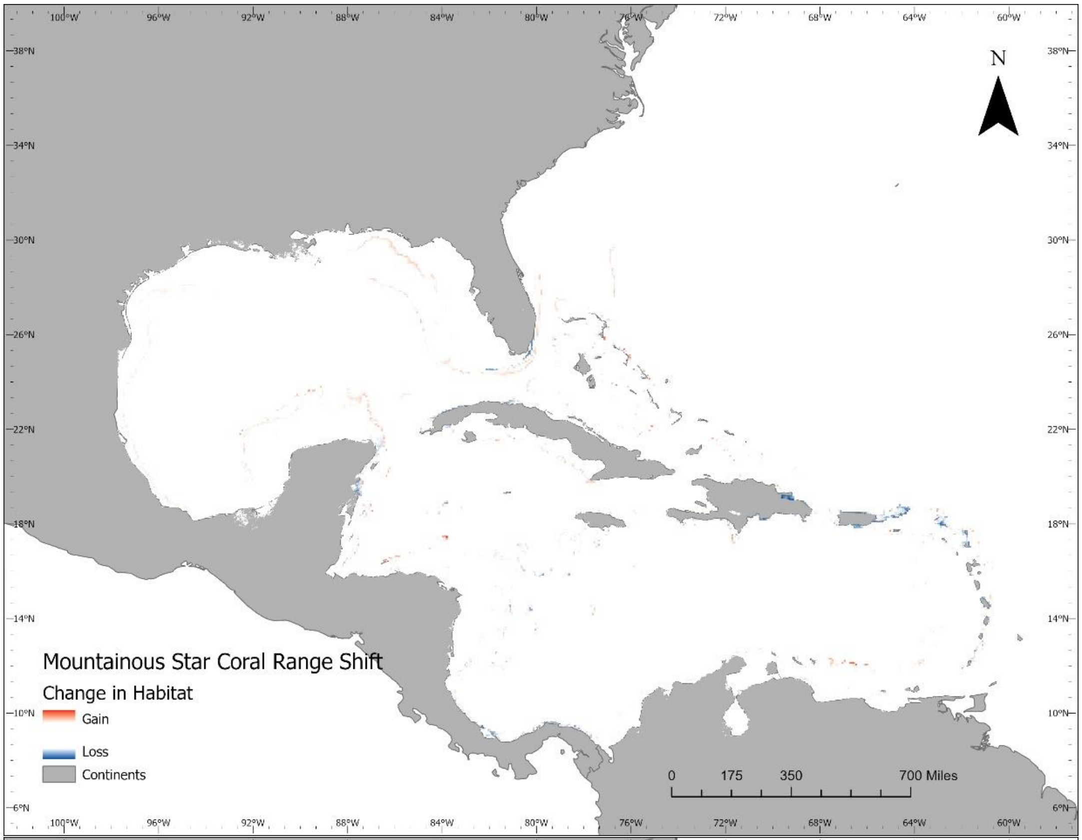

Knobby Brain Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

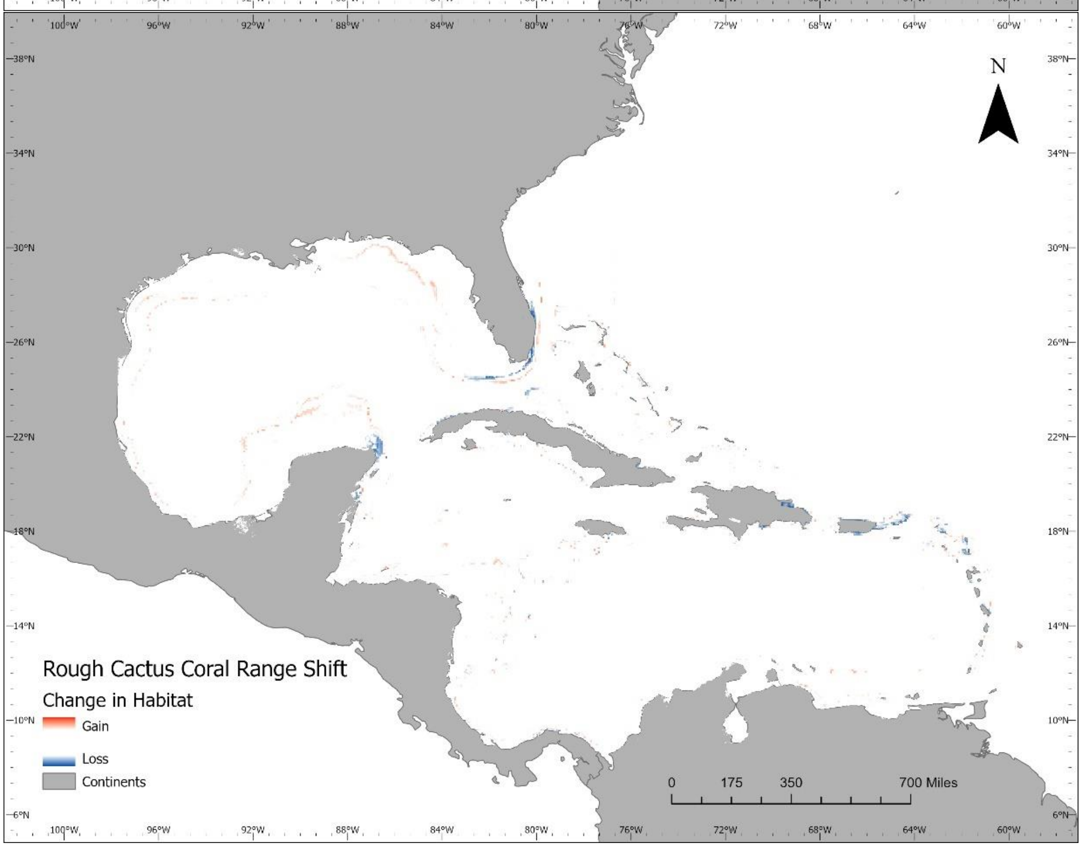

Lettuce Coral Range Shift
Change in Habitat
Loss
Gain
Continents
0 175 350 700 Miles
N

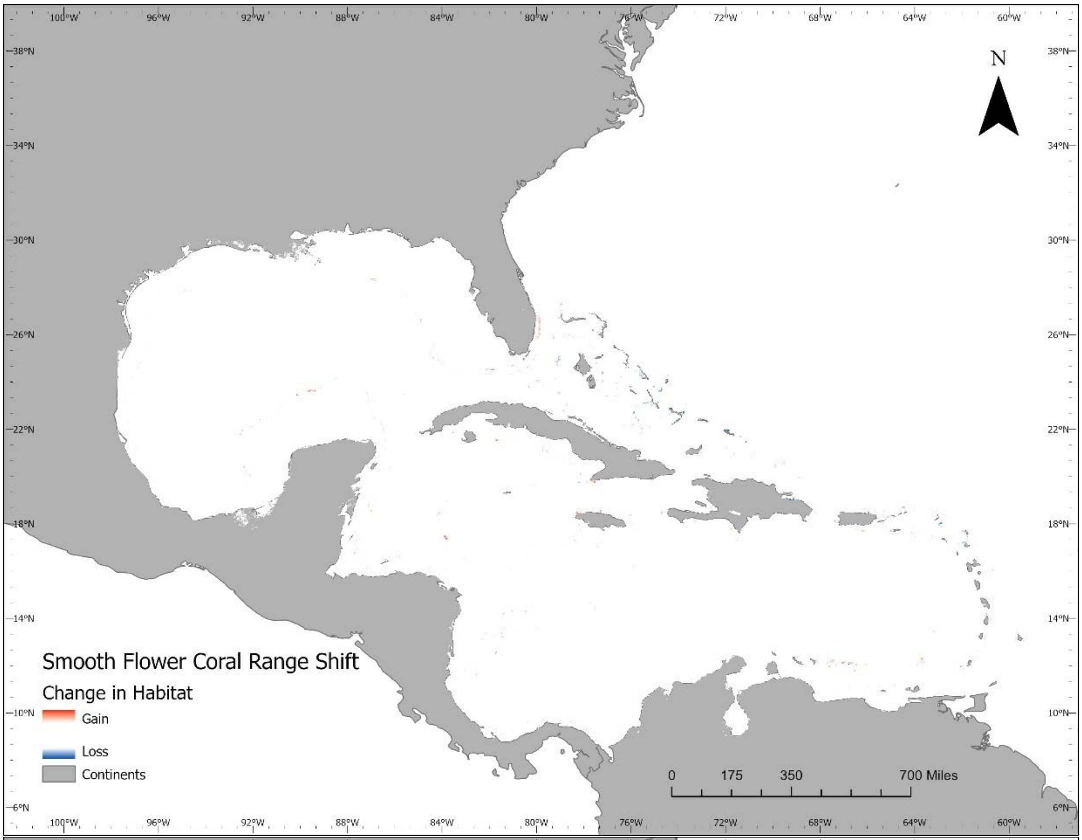

Lobed Star Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

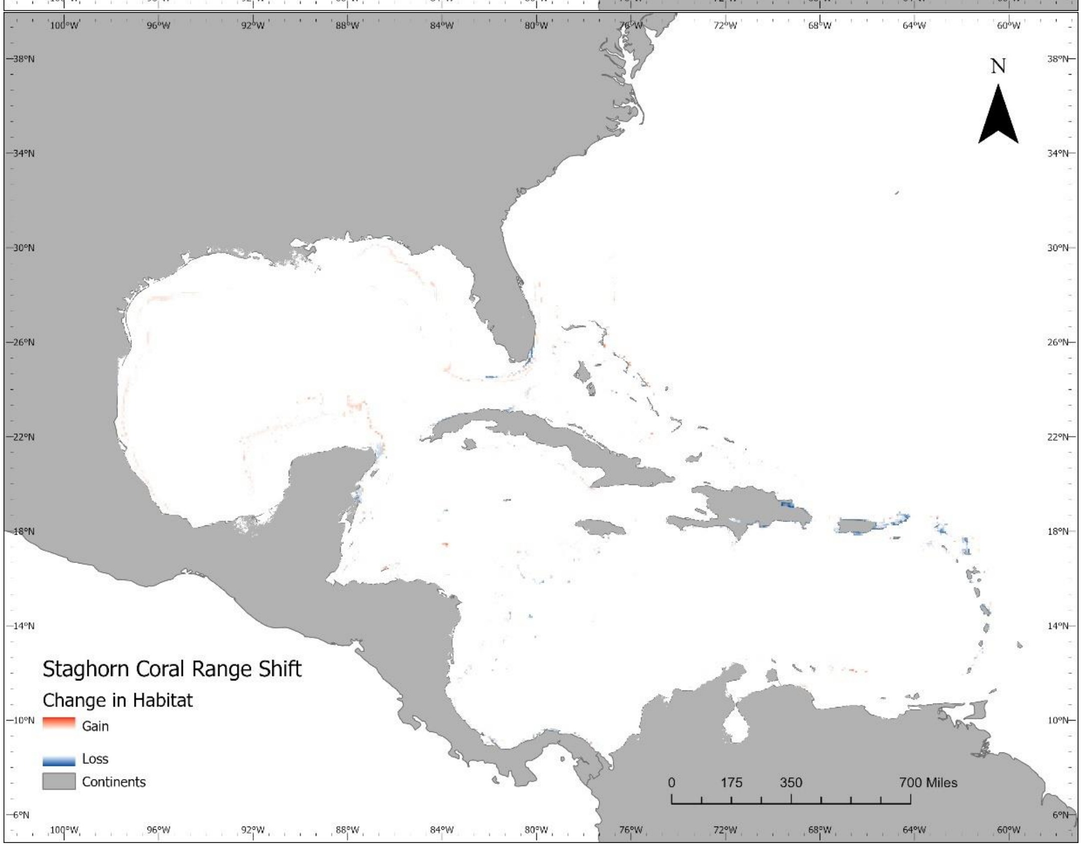

Massive Starlet Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N


Maze Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N


Mountainous Star Coral Range Shift
Change in Habitat
Gain
Loss
Continents
N
0 175 350 700 Miles


Rough Cactus Coral Range Shift
Change in Habitat
Gain
Loss
Continents
N
0 175 350 700 Miles


Smooth Flower Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N


Staghorn Coral Range Shift
Change in Habitat
Gain
Loss
Continents
0 175 350 700 Miles
N

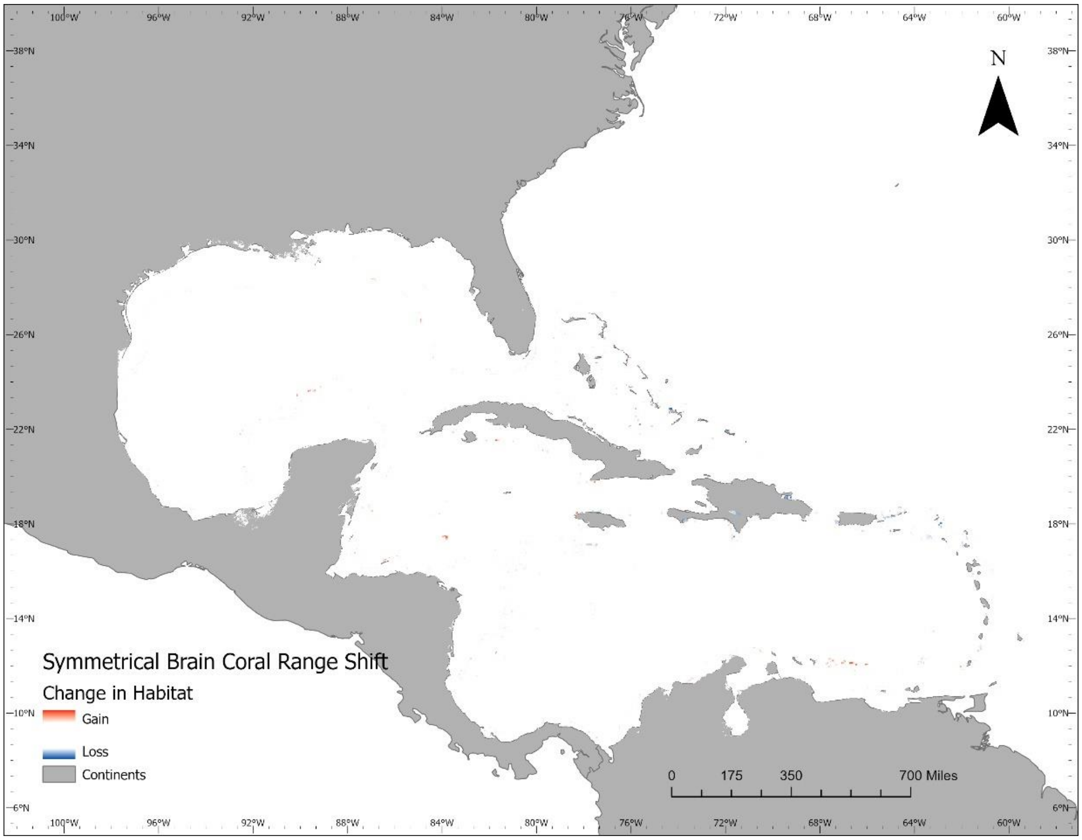

Symmetrical Brain Coral Range Shift
Change in Habitat
Gain
Loss
Continents
N
0 175 350 700 Miles
100°W
96°W
92°W
88°W
84°W
80°W
76°W
72°W
68°W
64°W
60°W
38°N
34°N
30°N
26°N
22°N
18°N
14°N
10°N
6°N

Table A1. Predicted suitability of coral habitats (% of suitable area) at present

	Not suitable	Low Suitability	Medium Suitability	High Suitability	Total
Acropora cervicornis	76.11	16.67	6.55	0.67	100
Acropora palmata	78.28	14.77	6.30	0.65	100
Dendrogyra cylindrus	75.45	17.50	6.21	0.84	100
Mycetophyllia ferox	76.49	17.26	5.58	0.66	100
Orbicella annularis	83.95	10.67	4.80	0.58	100
Orbicella faveolata	83.68	10.83	4.86	0.63	100
Orbicella franksi	76.87	16.23	6.17	0.74	100
Agaricia agaricites	0.77	59.58	25.07	14.59	100
Colpophyllia natans	1.21	54.13	27.83	16.84	100
Dichocoenia stokesii	34.05	36.98	15.67	13.29	100
Diploria labyrinthiformis	94.07	2.77	1.92	1.23	100
Eusmilia fastigiata	5.05	52.72	26.11	16.12	100
Meandrina meandrites	5.68	55.92	25.71	12.69	100
Montastraea cavernosa	93.51	3.35	2.09	1.04	100
Pseudodiploria clivosa	11.17	51.02	23.53	14.28	100
Pseudodiploria strigosa	34.09	34.09	20.32	11.49	100
Siderastrea siderea	35.35	35.35	19.57	9.74	100
Solenastrea bournoni	37.73	39.03	13.31	9.94	100
Stephanocoenia intersepta	6.09	60.65	22.59	10.67	100

Table A2. Predicted suitability of coral habitats (% of suitable area) in the future

	Not suitable	Low Suitability	Medium Suitability	High Suitability	Total
Acropora cervicornis	84.21	12.41	3.08	0.30	100
Acropora palmata	84.20	12.42	3.12	0.26	100
Dendrogyra cylindrus	87.40	10.62	1.85	0.14	100
Mycetophyllia ferox	85.42	12.55	1.93	0.10	100
Orbicella annularis	85.21	12.02	2.55	0.22	100
Orbicella faveolata	85.84	11.09	2.70	0.37	100
Orbicella franksi	85.40	11.47	2.89	0.24	100
Agaricia agaricites	0.97	66.21	24.41	8.41	100
Colpophyllia natans	1.83	58.26	24.97	14.94	100
Dichocoenia stokesii	32.64	37.31	16.22	13.83	100
Diploria labyrinthiformis	97.18	1.83	0.69	0.30	100
Eusmilia fastigiata	6.37	69.17	18.73	5.73	100
Meandrina meandrites	5.92	62.83	21.10	10.16	100
Montastraea cavernosa	92.69	4.53	2.00	0.78	100
Pseudodiploria clivosa	10.63	53.65	23.31	12.41	100
Pseudodiploria strigosa	93.62	4.16	1.63	0.59	100
Siderastrea siderea	91.60	5.03	2.45	0.91	100
Solenastrea bournoni	35.66	42.20	14.31	7.83	100
Stephanocoenia intersepta	6.53	62.34	21.37	9.76	100

Table A3. Calculated area of predicted coral habitat at present

		Area in million km^2			
	Not suitable	Low Suitabilit y	Medium Suitability	High Suitabilit y	Total
Acropora cervicornis	21.73	4.76	1.87	0.19	28.54982
Acropora palmata	27.65	5.22	2.22	0.23	35.32046
Dendrogyra cylindrus	16.97	3.94	1.40	0.19	22.4939
Mycetophyllia ferox	16.92	3.82	1.24	0.15	22.11616
Orbicella annularis	38.84	4.94	2.22	0.27	46.26296
Orbicella faveolata	35.26	4.56	2.05	0.27	42.13981
Orbicella franksi	20.59	4.35	1.65	0.20	26.79175
Agaricia agaricites	0.04	3.04	1.28	0.74	5.10399
Colpophyllia natans	0.07	2.99	1.54	0.93	5.5223
Dichocoenia stokesii	1.64	1.78	0.76	0.64	4.8216
Diploria labyrinthiformis	70.19	2.07	1.43	0.92	74.61142
Eusmilia fastigiata	0.24	2.49	1.23	0.76	4.71543
Meandrina meandrites	0.26	2.55	1.17	0.58	4.56797
Montastraea cavernosa	69.77	2.50	1.56	0.78	74.61142
Pseudodiploria clivosa	0.48	2.19	1.01	0.61	4.29255
Pseudodiploria strigosa	2.58	2.58	1.54	0.87	7.55892
Siderastrea siderea	3.05	3.05	1.69	0.84	8.62486
Solenastrea bournoni	1.36	1.41	0.48	0.36	3.60275
Stephanocoenia intersepta	0.31	3.06	1.14	0.54	5.04726

Table A4. Calculated area in million km^2 of predicted coral habitat in future

	Not suitable	Low Suitability	Medium Suitability	High Suitability	Total
Acropora cervicornis	26.86	3.96	0.98	0.10	31.89419
Acropora palmata	30.43	4.49	1.13	0.09	36.13823
Dendrogyra cylindrus	21.49	2.61	0.46	0.03	24.58732
Mycetophyllia ferox	19.15	2.81	0.43	0.02	22.41743
Orbicella annularis	31.18	4.40	0.93	0.08	36.59168
Orbicella faveolata	30.74	3.97	0.97	0.13	35.81409
Orbicella franksi	23.60	3.17	0.80	0.07	27.63199
Agaricia agaricites	0.05	3.50	1.29	0.44	5.28095
Colpophyllia natans	0.10	3.12	1.34	0.80	5.35014
Dichocoenia stokesii	0.98	1.12	0.49	0.41	2.99032
Diploria labyrinthiformis	72.51	1.36	0.51	0.23	74.61142
Eusmilia fastigiata	0.21	2.25	0.61	0.19	3.25864
Meandrina meandrites	0.23	2.42	0.81	0.39	3.84757
Montastraea cavernosa	69.15	3.38	1.49	0.58	74.61142
Pseudodiploria clivosa	0.47	2.35	1.02	0.54	4.38825
Pseudodiploria strigosa	69.85	3.10	1.22	0.44	74.61142
Siderastrea siderea	68.35	3.75	1.83	0.68	74.61142
Solenastrea bournoni	1.49	1.76	0.60	0.33	4.17368
Stephanocoenia intersepta	0.18	1.72	0.59	0.27	2.75359