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RESEARCH ARTICLE

Habitat suitability models of elkhorn coral provide ecological insight to support coral reef restoration

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Coral reefs are experiencing unprecedented levels of stress from global warming, ocean acidification, fishing, and water pollution. In the Caribbean and Western Atlantic, multiple stressors have resulted in widespread losses of the dominant reef-building Acroporid corals, two of which are listed as threatened species under the 1973 U.S. Endangered Species Act. In response, active coral reef restoration through the outplanting of live corals has become a widespread intervention technique. To increase restoration success, active coral reef restoration requires significant investment and careful planning, and selection of suitable sites for coral outplanting is an essential early step with considerable influence on restoration outcomes. We applied a maximum entropy model to predict and map habitat suitability for the reef-building coral species, *Acropora palmata*, around the island of St. Croix in the U.S. Virgin Islands. Based mostly on bathymetry and benthic habitat type, the highest performing model predicted approximately 21.75 km^2 of the highest probability of suitable habitat, of which over half occurred within existing marine protected areas (MPAs). Outplanted coral at 60% of sites coincided with predicted maximum habitat suitability index values greater than 0.75 and 35% with values greater than 0.90. The model reveals that all three statutory MPAs with shallow water coral reefs have a considerable area (13.24 km^2) of predicted high suitability seabed with potential for active *A. palmata* restoration efforts. The predictive spatial modeling approach provides a cost-effective tool to inform future coral restoration design and to evaluate the habitat suitability of coral outplanting sites.

Key words: *Acropora palmata*, coral reefs, habitat suitability, maximum entropy, predictive mapping, site selection

Implications for Practice

- Demonstrating how predictive habitat suitability modeling can be employed at relatively fine spatial scales to identify potential portfolios of coral outplanting sites.
- Outlining how the results of this modeling approach can be combined with expert opinion at various stages to streamline and support current techniques for coral outplant site selection at low cost.
- An evaluation of current and planned outplanting sites in St. Croix, highlighting potential adjustments for conservation managers to employ to capture higher proportions of suitable habitat and therefore maximize outplant survival.
- Highlighting current data deficiencies (particularly in regard to biophysical variables and high-resolution environmental data) to encourage continued effort in the development of novel data collection techniques in marine settings.

Introduction

Globally, coral reefs are experiencing severe threats from a combination of anthropogenic influences at a range of spatial and temporal scales (Hughes et al. 2018). The Intergovernmental Panel on Climate Change (IPCC) predicts that at global warming of 1.5°C above pre-industrial levels could result in the loss of up to 90% of the world's coral, and at 2°C of warming many corals will become extinct (IPCC 2018). Rising sea temperatures and resultant thermal stress events pose the most significant widespread threat to shallow water corals (Williams et al. 2017; Guan et al. 2020). In the Caribbean, thermally

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stressed corals have shown susceptibility to disease following marine heatwaves (Rogers 2009), as well as being impacted by a variety of threats including nutrient loading and contaminants from land-based sources (Wirt et al. 2013), invasive species (e.g., Hixon et al. 2016), and fishing that can diminish the regulatory functions provided by fish (Valdivia et al. 2017; Shantz et al. 2020). Each factor's relative importance varies both temporally and spatially, but Guan et al. (2020) suggested that 61% of all corals worldwide are currently under threat from both local and global stressors and 94% are under threat from at least one of these. The cumulative stressors operating on corals at both global and local scales mean that both effective protection that mitigates threats to corals and active restoration are urgently required to secure a long-term future for coral reefs (Hoegh-Guldberg et al. 2018; Donovan et al. 2021).

Loss of coral reefs can have widespread consequences for tropical coastal ecosystems through reductions in structural complexity of habitats for reef-dwelling species (Alvarez-Filip et al. 2009; Rogers et al. 2014). The ecological impacts from loss of living structure are exacerbated by the fact that Caribbean coral reef communities exhibit a relatively low functional redundancy (Micheli et al. 2014), meaning a decline or loss of ecosystem engineer species can result in long-lasting transformative ecological change (Mora et al. 2016; Estrada-Saldívar et al. 2019; Toth et al. 2019). In addition, coral reef decline has important implications for humans through the loss of diverse and valuable ecosystem services (Eddy et al. 2021). For instance, ecosystem services associated with coral reefs in the U.S. Virgin Islands (USVI) have been estimated to be worth as much as $200 million annually (van Beukering et al. 2011).

As a result of multiple interacting stressors to Caribbean coral reefs, including white-band disease outbreaks, ocean warming, and human activity, there is an increased awareness of the necessity to mitigate stressors and to actively restore coral reefs rather than just protecting those that remain in algal-dominated states (Nyström et al. 2012). Although the most significant driver of coral loss globally is ocean warming (Hughes et al. 2018), localized restorative actions can support the resilience of coral reefs by ensuring stressors are mitigated and reefs are re-populated with living coral colonies (Cinner et al. 2016; Bayraktarov et al. 2019; Anthony et al. 2020). Active restoration in this context is defined as the assisted recovery of degraded ecosystems through active human intervention, most commonly in the form of coral gardening (Bayraktarov et al. 2016). In the Caribbean alone, more than 150 coral restoration projects are now underway across more than 20 countries (Foo & Asner 2019). The process of coral outplanting requires significant investment of capital and resources. For instance, based on a global sample of 87 coral restoration projects, Bayraktarov et al. (2019) estimated a median cost of around $400,000/ha. Minimizing the costs associated with outplanting and optimizing the long-term success of restoration is crucial for attracting the investment needed to scale up active coral reef restoration projects.

Understanding the distribution of species-specific spaces and the most suitable outplanting sites to optimize coral growth, survival, and socioeconomic feasibility is an essential step in designing efficient and reliable coral restoration programs (Schopmeyer et al. 2017). McClanahan et al. (2009) highlighted that some coral reefs, termed "reefs of hope," have a significantly greater likelihood of restoration success than others based on environmental and ecological conditions operating at a range of spatial and temporal scales. At broad spatial scales (10s to 100s of km^2), such as selecting which islands to focus ecological restoration efforts at, the most important factors are often ocean temperatures and warming forecasts, disease prevalence, existing coral cover, wave exposure, larval connectivity, storm occurrence, and water quality (Foo & Asner 2019). For selecting specific sites for coral restoration at the within-island scale, a wide range of other factors will also come into play such as nutrient loading, predation, competition, bathymetry, benthic habitat type, contaminants, turbidity, salinity, and other human activity including boat traffic, anchoring, and fishing (Hernández-Delgado et al. 2014; Foo & Asner 2019). The biophysical information requirements pose a decision support challenge since reliable high-resolution spatial data on many of these biophysical predictors are not widely available for coastal areas (Robinson et al. 2011). Furthermore, suitable data for understanding dynamic processes and past conditions are often unavailable. In the absence of extensive empirical data on difficult to measure variables, there is a need to produce reliable spatial proxies and advance spatial analytical approaches which can be used to inform site selection. Indeed, new remote sensing methods are delivering unprecedented performance in high spatial resolution data for shallow coastal seascapes (Hedley et al. 2016; Purkis 2018). These technological advances in remote sensing combined with high-performing predictive modeling techniques provide analytical tools to predict habitat suitability using a combination of spatial proxies for unmeasured ecological patterns and processes (Sekund & Pittman 2017; Schill et al. 2021a, 2021b). However, few studies have applied these spatially explicit ecological approaches to coral restoration.

Our work advances the mapping of critical habitat conducted by Wirt et al. (2015) that identified and mapped potential habitat for *Acropora* corals in Florida and the U.S. Caribbean by overlaying historical records of *Acropora palmata* (elkhorn coral) and *A. cervicornis* (staghorn coral) presence (10 and 30 m, respectively) on shallow benthic maps. This analysis identified broadly defined depth-constrained geographical distributions where *Acropora* spp. would be expected to be found (Wirt et al. 2015). To refine the accuracy and resolution of habitat suitability, we applied maximum entropy (MaxEnt) modeling (Elith et al. 2011), a machine learning algorithm, to model and map habitat suitability predictions for *A. palmata* around St. Croix. In this case, MaxEnt predicts habitat suitability by calculating the probability of presence using the statistical relationships between locations of historical presence records and multiple environmental predictors relevant to *A. palmata* ecology. The resultant spatially explicit predictions of suitable elkhorn coral habitat were intended to inform spatial prioritization in site selection for coral outplanting, evaluate the suitability of existing restoration sites, and support the planning process for the scaling up of coral restoration projects. Specifically, MaxEnt was applied to model and map the species' realized niche (i.e. the range of environmental conditions that determine where the species is found) across the entire geographical extent of the environmental data (Lauria et al. 2015; Melo-Merino et al. 2020). Although habitat suitability modeling has been applied to map species distributions of cold-water corals (Davies & Guinotte 2011), this approach has seen far fewer applications to support conservation strategies for the highly vulnerable corals in shallow tropical coastal waters (Pittman et al. 2009; Pittman et al. 2018; Egan et al. 2021).

Here, we address two research objectives:

(1) To apply habitat suitability modeling to quantify a realized environmental niche and assess the relative contribution of environmental variables for predicting the suitability of potential *A. palmata* habitat around St. Croix (USVI).
(2) To apply the model results to better understand the potential portfolio of locations that restoration projects in St. Croix could consider for future *A. palmata* outplanting, as well as to assess the suitability of existing outplanting sites.

Methods

Study Area and Focal Species

Acropora palmata, a relatively fast-growing branching coral, is one of the most important reef-building corals in the Caribbean, typically occupying reefs at depths shallower than 5 m, with a relatively low heat tolerance of temperatures above 29°C (Jaap et al. 1989). Jackson et al. (2014) estimated that *A. palmata* once covered 85% of shallow (<5 m depth) Caribbean reefs, but now around 95% have been lost. As such, this species has been classified as critically endangered by the IUCN (2008) and is listed as threatened under the U.S. Endangered Species Act (2006). *Acropora palmata* has been identified as a target for coral reef restoration not only because of its endangered condition and vital ecological role in Caribbean reefs, but also because this species is well suited to the requirements of restoration projects since it reproduces primarily by fragmentation and has relatively fast growth rates (Schopmeyer et al. 2017).

St. Croix (Fig. 1) is the largest and southernmost of three major islands in the USVI and has experienced one of the most dramatic Acroporid coral die-backs in the Caribbean, primarily due to the rapid emergence of white-band disease and marine heatwaves (Miller et al. 2009). Mayor et al. (2006) estimated that since 1970, St. Croix has lost around 90% of its *Acropora* coral populations. Hurricanes Maria and Irma in 2017 also damaged many coral reefs in this area (Viehman et al. 2020). As a result, St. Croix has become one of the leading sites for investment in *Acropora* coral restoration in the Caribbean using both asexual and sexual recruitment techniques (Moulding et al. 2020). The Nature Conservancy, for instance, has outplanted more than 25,000 nursery-grown Acroporid corals since 2012 (The Nature Conservancy 2018) with most effort located in the northeast of St Croix. Although St. Croix hosts several marine protected areas (MPAs) that encompass coral reefs, long-term monitoring of live coral cover has revealed few signs of recovery from cumulative impacts (Pittman et al. 2014), largely due to a lack of systematic restoration procedure, poor site selection, and hurricane activity. Additionally, other locally designated Areas of Particular Concern exist but are not yet effectively managed MPAs.

Coral Species Occurrence Data

Georeferenced species occurrence data (reported between 2000 and 2021) for *A. palmata* were acquired from multiple open access data repositories: the Ocean Biodiversity Information System (OBIS 2019), the Global Biodiversity Information Facility (GBIF 2021), the U.S. National Oceanic and Atmospheric Administration's Coral Reef Conservation Program, and the Nature Conservancy and University of the Virgin Islands Conservation Data Center. Only in situ observations were used in the model (as opposed to museum samples or relict specimens), and duplicate observations were removed resulting in 1,954 occurrence records for *A. palmata* around St. Croix (Fig. 2). Outplanted corals were not included in the occurrence records to avoid bias in restoration sites which may or may not contain suitable habitat for *A. palmata*. Additionally, occurrence records were concentrated on the study area's northeast portion, creating a geographical bias (Fig. 2). Following Stuart et al. (2021), a bias file using a Gaussian kernel density surface (Bowman & Azzalini 1997) was applied to MaxEnt models to account for spatial biases in the sampling effort.

Environmental Predictors

Environmental data for the marine areas around St. Croix were selected to quantify and map the spatial characteristics of the seafloor terrain and the distribution of benthic habitat types, as well as water conditions (Table 1). Satellite-derived bathymetry modeled at 10 m resolution (Li et al. 2021) was obtained from the Allen Coral Atlas (2022) (https://allencoralatlas.org). Bathymetry was only available where the seafloor was reliably detected in optical satellite images (<25 m depth). Depth validation points from bathymetry transects (41,500 for St. Croix) were highly correlated ($r^2 = 0.79$; residual mean square error = 1.60) with satellite-derived depth (Li et al. 2021). Reported errors were higher in deep waters (>15 m) and clusters of data gaps occurred across the deeper waters (>20 m) of the eastern insular shelf. The habitat map was also validated using a georeferenced benthic photoquadrat approach carried out during field surveys (Roelfsema et al. 2021).

Benthic Seascape Structure

Surface pattern metrics were applied to the bathymetric data to quantify surface geomorphology (i.e. slope, cosine aspect [south–north], sin aspect [west–east]) using the Benthic Terrain Modeler tool version 3.0 in ArcGIS with a 3 × 3 window of moving cells (Walbridge et al. 2018). Topographic complexity of the seafloor terrain was quantified as the slope-of-slope, a measure of the change in slope (Pittman et al. 2009) within a 3 × 3 analytical window using ArcGIS Spatial Analyst. Benthic habitat was represented by a benthic habitat map with 12 patch types covering shallow (<30 m depth) nearshore coral reef ecosystems. The map was produced by the Nature Conservancy for

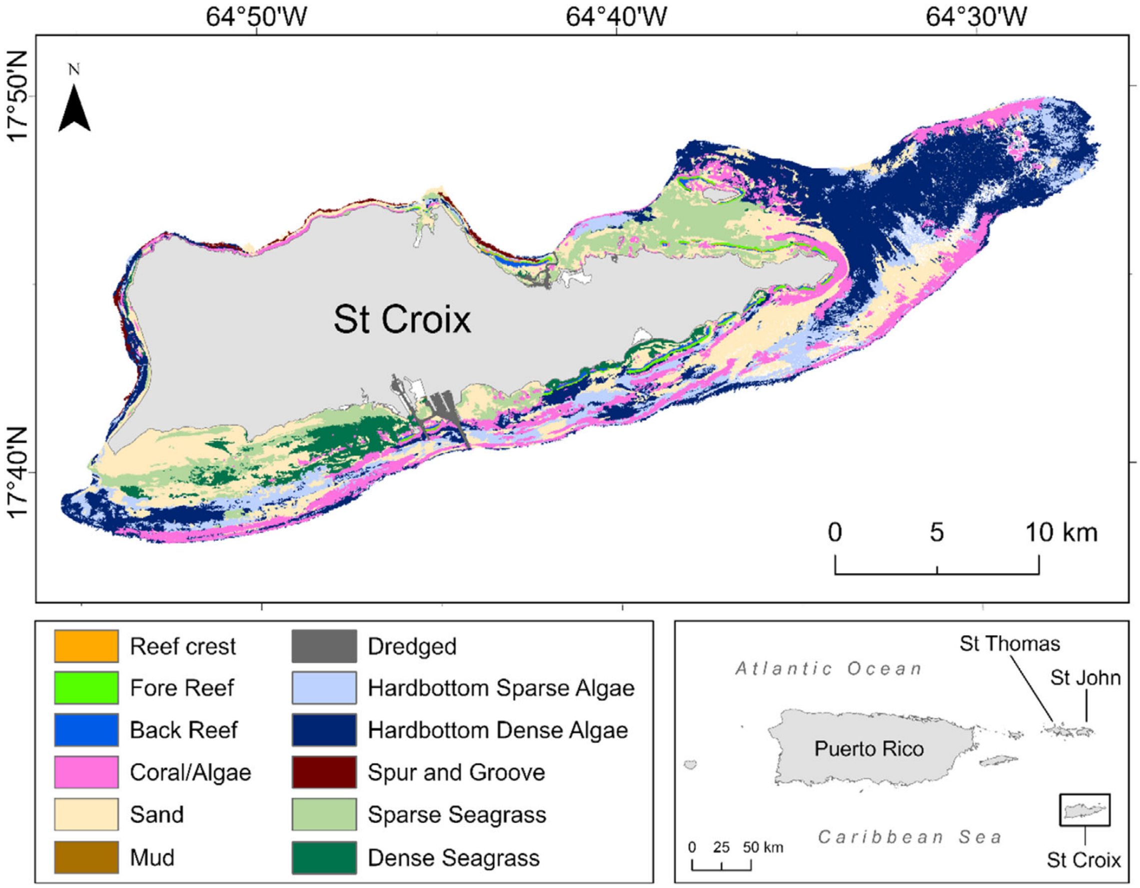

Figure 1. Benthic habitat classes mapped for shallow waters (<25 m depth) around St. Croix (U.S. Virgin Island) using object-based classification of very high-resolution satellite data. Source: The Nature Conservancy (https://sites.google.com/view/caribbean-marine-maps)

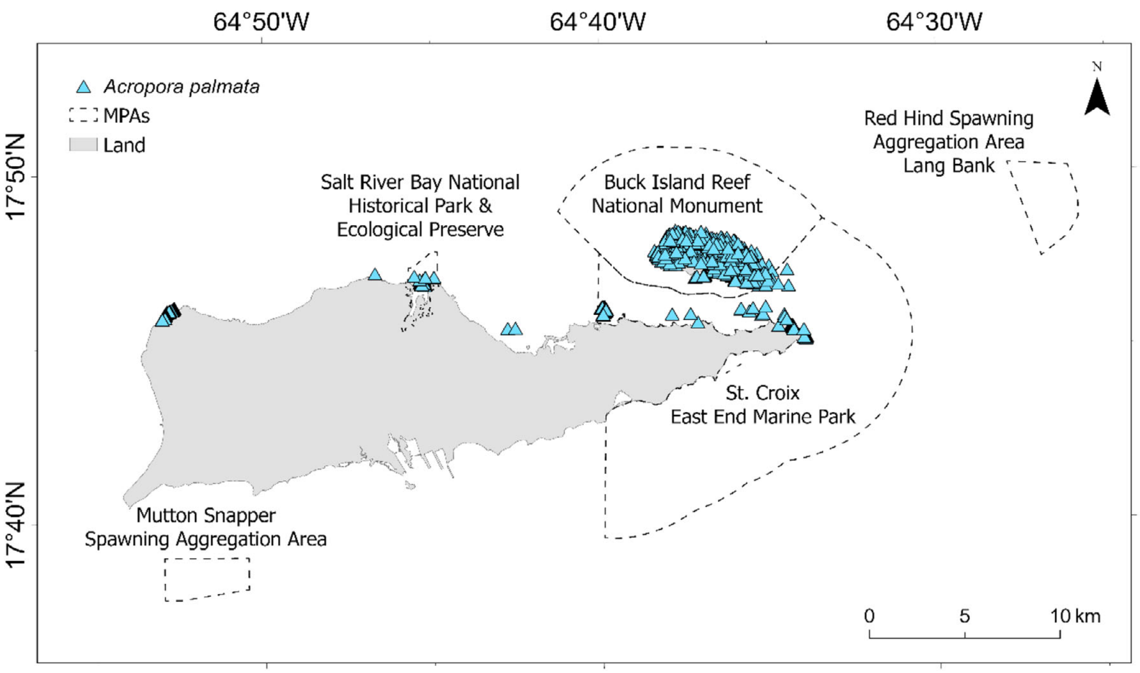

Figure 2. *Acropora palmata* occurrence data (blue triangles) used in MaxEnt models and the boundaries of existing MPAs around St. Croix.

Table 1. Explanatory variables used in MaxEnt modeling after unsuitable variables were rejected.

Variable	*Units*	*Data Source*	*Definition*
Water depth	Meters	Allen Coral Atlas (all at 10 m^2 resolution)	Depth of water to the seafloor in meters
Cosine aspect	South (<0) to north (>0)		The cosine of the compass direction of a point's slope (in degrees), giving a value for south–north aspect
Sin aspect	West (<0) to east (>0)		The sine of the compass direction of a point's slope (in degrees), giving a value for west–east aspect
Slope-of-slope	Degrees of degrees		A measure of the maximum rate of maximum slope change (topographic complexity)
Slope	Degrees		A measure of the gradient of the seafloor at a point
Benthic habitat types	Categorical (12)	Schill et al. (2021b) (https://sites.google.com/view/caribbean-marine-maps)	Categorical data with 12 different classifications of benthic habitat types around St. Croix
Mean summer temperature	Degrees Celsius	U.S. Environmental Protection Agency Water Quality Portal	Average surface temperature of ocean waters from July to September in °C
Mean summer salinity	Practical salinity units		Average concentration of ocean water salts from July to September in ppt (parts per thousand)

the insular Caribbean with object-based image analysis applied to very high (<5 m) resolution Planet Labs "Dove" satellite imagery yielding an overall map accuracy of 80% (Schill et al. 2021b). For St. Croix, the classification algorithm was trained (50% of data) and validated (50% of data) using 1,372 georeferenced field reference points from underwater video transects acquired in the same years as satellite images (2017–2019) used for benthic mapping. Bathymetric data were also collected along video transects. The benthic map was used as the area of interest for the predictive mapping.

Water Conditions

All water parameter data were obtained using the Water Quality Portal of the U.S. National Water Quality Monitoring Council (https://www.waterqualitydata.us/), which collates data from the U.S. Geological Survey, the U.S. Environmental Protection Agency, and local government agencies. Data on water conditions included sea surface temperature, salinity, turbidity, pH, nitrate concentrations, phosphate concentrations, and photosynthetically active radiation (PAR; see Supplement S1). To account for the nonuniform temporal distribution of site measurements, water quality data were divided into summer and winter readings, and these were filtered to only include sites with more than five unique years with data since 2000. Any datasets that were left with insufficient data points after this process were rejected. The remaining data, coming entirely from 2015 to 2021, were then tested independently for spatial autocorrelation using Moran's I with both normal approximations and Monte Carlo permutations (Bowman & Azzalini 1997). Any datasets that failed to show statistically significant spatial autocorrelation ($p \leq 0.05$) were rejected as this autocorrelation is a fundamental requirement for an appropriate interpolation. Next, multicollinearity among spatial predictors was examined with a Pearson correlation matrix and tested with the variance inflation factor (VIF). Variables with VIF >5 were removed. The point-based datasets for summer salinity and mean summer temperature were then rasterized in RStudio version 8.16 using an empirical variogram model to a resolution of 10 m^2 to match bathymetry data downloaded from the Allen Coral Atlas (2022).

Predictive Mapping With MaxEnt

MaxEnt version 3.4.4 (Phillips et al. 2006) was used to model and map the relative probability of *A. palmata* occurrence interpreted here as an index of relative habitat suitability (Fig. 3). The *A. palmata* model applied 10-fold cross-validation (Anakha et al. 2021), with each replicate using a random selection of 900 occurrence points for training and the remaining points for testing, with an average calculated across all models (Rengstorf et al. 2013). The environmental conditions at *A. palmata* occurrence sites were compared to those at 10,000 background sites selected in accordance with the bias file, and linear, quadratic, product, and hinge features were used.

Model evaluation was carried out using the receiver operating characteristic (ROC), the area under the curve (AUC), and average omission. The former quantifies the discrimination capacities of the model, or in other words, the model's ability to discern presence points from background points (Wan et al. 2019). An AUC value of 0.5 indicates that a model is no better than random at discerning presence points from background points, and the closer this value is to 1, the stronger the model performance is. Average omission estimates the model's likelihood of producing false absences at different cumulative thresholds. Percent contribution and permutation importance were used as metrics in our model assessment to evaluate the relative importance of each explanatory variable. The former describes the marginal increase in regularized gain as each variable is independently introduced to the model during the training phase, and the latter is a measure of the percentage drop in AUC when a randomly scrambled version of each variable dataset is used instead of the actual datapoints in the final model.

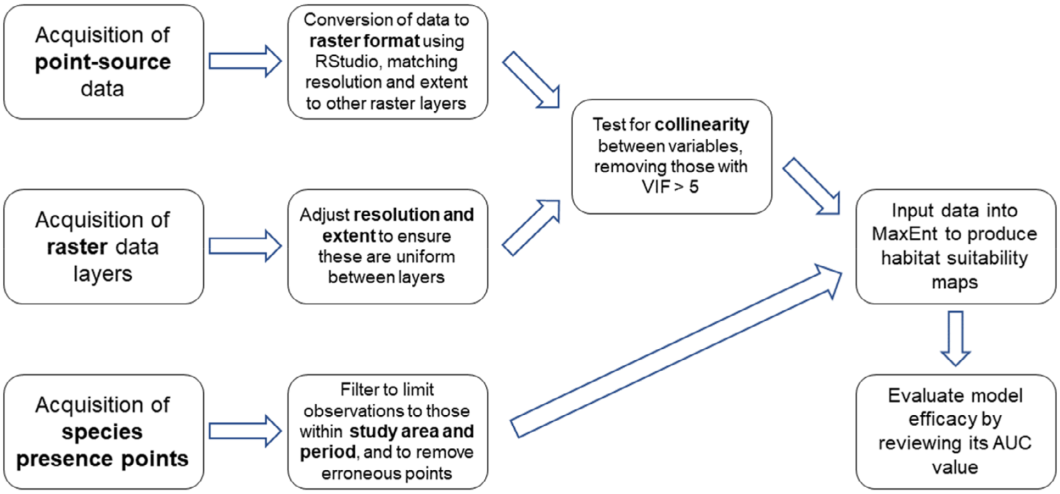

Figure 3. Workflow summarizing the steps taken in data processing and habitat suitability modeling using MaxEnt.

Quantifying Habitat Suitability for Historical and Future Outplanting Sites

To evaluate the suitability of habitats surrounding existing *A. palmata* restoration sites, we extracted the predicted habitat suitability scores at 20 georeferenced outplanting sites along St. Croix's northern shore obtained from NOAA's Coral Reef Conservation Program (CRCP) between 2012 and 2021 (O'Connor et al. 2020). Sites were buffered to create an analytical window of 30-m radius (2,827 m^2) around each point using the Pairwise Buffer tool in ArcGIS Pro version 3.1.0 to encompass any potential geopositional errors when the historical outplanting sites were georeferenced with a global positioning system. Information on survivorship and other biological indicators of coral response, such as growth rates and resilience to stressors was unavailable for outplanting sites due to the short-term monitoring of most restoration projects to date.

The locations of four planned future restoration sites—Long Reef, Sweepers Complex, Llews Reef, and Butler Bay—were also obtained as a polygon data layer (Henderson 2022, personal communication) for evaluation. These sites were selected based on expert knowledge and local stakeholder consultation by evaluating a diverse set of strengths and weaknesses, opportunities, and threats. To assess habitat suitability for *A. palmata* within these polygons, the percentage and total area of each site polygon classified as highly suitable habitat (defined here as >0.75 habitat suitability index [HSI]) was calculated using ArcGIS Pro version 3.1.0.

Results

Selection of Spatial Predictors

Several water quality metrics were rejected from this analysis due to insufficient data points or a lack of spatial autocorrelation required for successful interpolation. Therefore, the variables used in the MaxEnt model were bathymetry and bathymetric derivatives including cosine aspect, sin aspect, slope, slope-of-slope, benthic habitat, mean summer temperature, and mean summer salinity (Table 1). A Pearson's correlation matrix found no significant pairwise correlations among predictor variables (Fig. S1).

Model Performance

We used the AUC and average omission of our predictive model to assess the model's ability to capture presence points accurately. The average model result produced an AUC value of 0.820 (3 significant figures), indicating good model performance. The average omission plot also showed a strong linear increase in fractional value with cumulative threshold, further confirming strong model performance.

Quantifying the Environmental Niche for *A. palmata*

Response curves (Fig. 4) indicated that habitat suitability peaked at depths of approximately 10 m, but moderately suitable habitats (>0.5 relative HSI) were predicted for depths between 3 and 12 m. Spur and groove (high relief colonized hardbottom), hardbottom with dense algae (including gorgonians and hard corals), and dense seagrass patch types produced the highest relative habitat suitability. High suitability habitat predicted for areas of dense seagrass, however, produced very high uncertainty estimates. Habitat suitability was markedly lower where mean summer temperatures were greater than 29.6°C, and peaked at mean summer salinities of 34.75 PSU. However, a small range of salinity in the study area hinders any interpretation of influence on suitability. *A. palmata* suitability appeared to increase with higher values of both slope and slope-of-slope, but both variables contributed relatively little to the final model. The plots for cos aspect and sin aspect were excluded as none of the metrics used for model evaluation suggested that these variables played a significant role in determining habitat suitability for *A. palmata*.

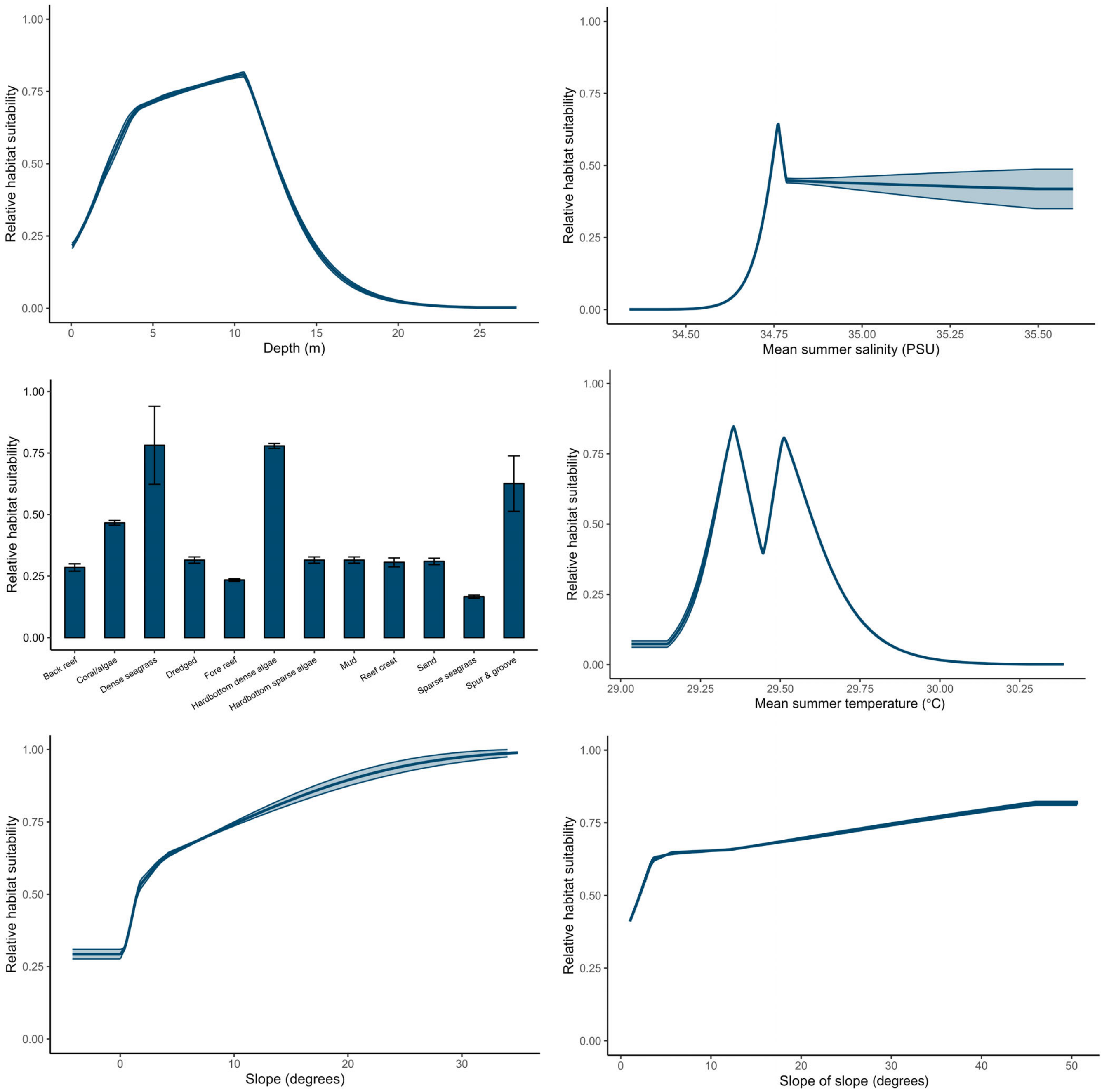

Figure 4. Model response curves for bathymetry, mean summer salinity, benthic habitat, mean summer temperature, slope, and slope-of-slope based on the *Acropora palmata* model runs. Buffer areas around the plots show the mean ±1 SD.

Identifying Possible Restoration Sites Based on Habitat Suitability Mapping

Mapping the habitat suitability estimates produced by averaging all 10 replicate MaxEnt models for *A. palmata* illustrates the distribution of potentially suitable habitat and restoration sites for this species around St. Croix (Fig. 5). The model predicted some concentrated areas of high suitability along the reefs of the island's northeast coast, where restoration efforts to date have been focused. However, significant hotspots of suitable habitat were also identified along the island's southeast, north, and west coasts. There was also a significant area of highly suitable habitat along the northern portion of Buck Island Reef National Monument. Standard deviations between model runs were generally low, with the greatest variability observed along the south coast (Fig. 5).

Relative Importance of Environmental Factors

The environmental predictors' percentage contribution and permutation importance values varied considerably (Table 2).

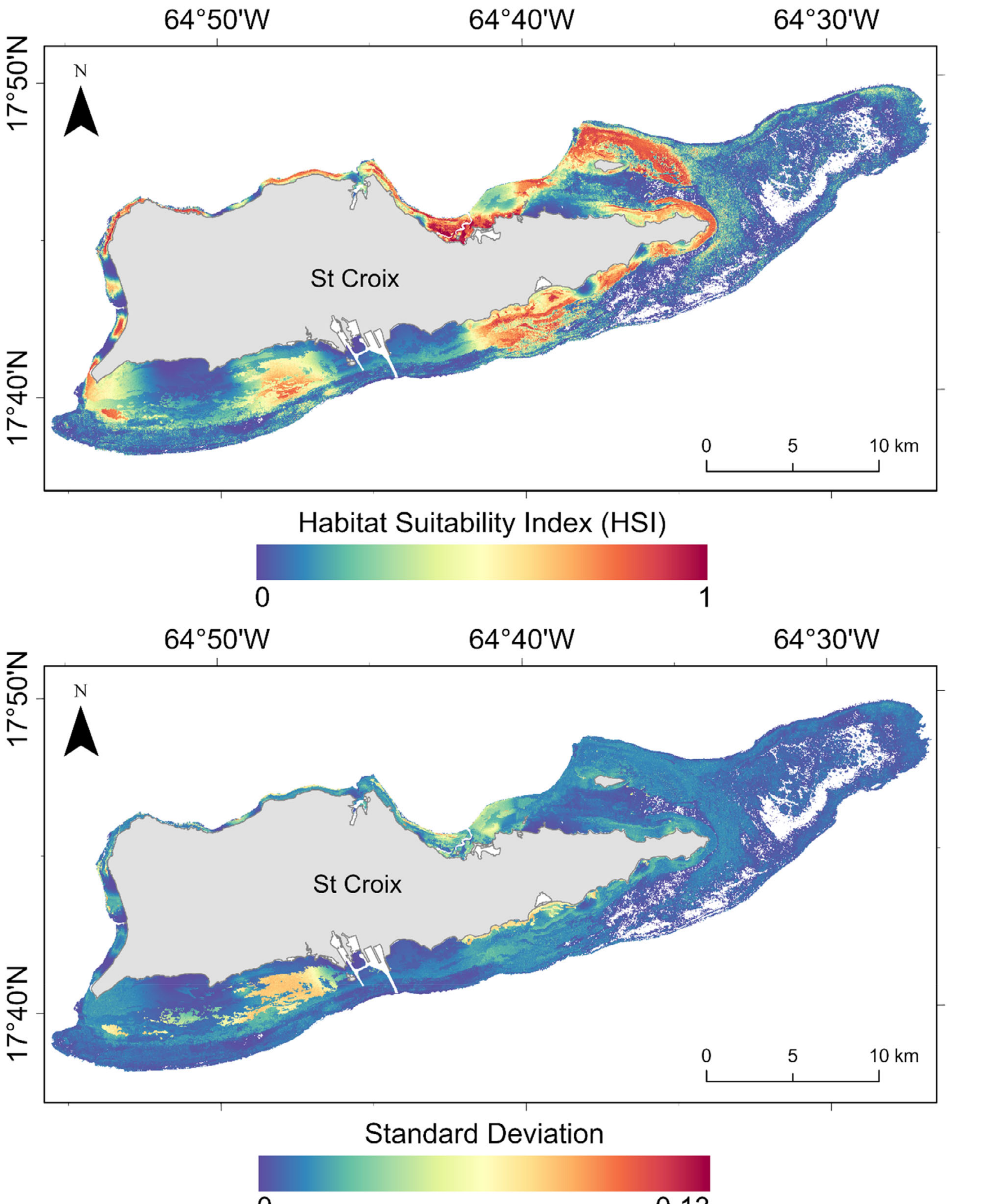

Figure 5. Maps showing aggregated predictions from the 10 replicate MaxEnt simulations of habitat suitability index (HSI) for *Acropora palmata* on St. Croix and standard deviation of HSI values per cell between the 10 replicate MaxEnt models. White spaces are no data pixels at depths beyond the limits of the bathymetric dataset.

Some predictors contributed more during the training of the model, as represented by their percent contribution values, whereas others were found to be more important as predictors in the final model. For example, the benthic habitat type had a relatively high percent contribution during training of 20.9%, but just a 2.6% permutation importance, whereas the opposite was true of mean summer temperature (6.4 and 33.5%, respectively). However, both percentage contribution and permutation importance metrics indicate that water depth contributed most to the *A. palmata* model. Mean summer salinity also had a relatively high percent contribution of 16.8%. The other variables included in the model made only minor contributions to model predictions.

Where High Suitability *A. palmata* Habitat Is Protected

The presence of well-managed MPAs provides a potential opportunity for greater threat mitigation from local stressors. One of the largest continuous areas (6.54 km^2) of high suitability *A. palmata* habitat inside an MPA was predicted for nearshore waters of St. Croix East End Marine Park, where much of the active coral restoration has already occurred. Buck Island Reef National Monument also encompassed a similarly large area (6.58 km^2) of high suitability habitat. Approximately 2.9% of the Salt River Bay National Historic Park and Ecological Preserve area was predicted as high suitability habitat for *A. palmata* (Table 3). The combined highly suitable shallow water area for *A. palmata* inside statutory MPAs amounts to 13.24 km^2. The two deeper water offshore fishery management areas had comparatively few high suitability cells due to being located in deeper waters near the shelf edge.

Habitat Suitability of Historical *A. palmata* Outplant Sites

Predictions of *A. palmata* habitat suitability at 20 existing coral outplanting sites (2012–2021) on St. Croix (Fig. 6) indicated high and variable HSI scores (mean 0.80 ± 0.19 SD). Most outplanting sites (12 of 20) coincided with a seascape maximum HSI score greater than 0.75 and 7 of 20 coinciding with HSI greater than 0.9.

Habitat Suitability of Planned Restoration Sites

The four planned outplanting sites were found to have varying levels of habitat suitability (Fig. 7), ranging from 0.4% highly suitable area at Sweepers Complex to 54.5% at Butler Bay (Table 4). Overall, these four sites were estimated to contain 408,300 m^2 of highly suitable area, representing 38.4% of the total area of these sites, indicating strong agreement between predicted high suitability reefs and sites selected through the expert and stakeholder-led site selection.

Table 2. Percent contribution and permutation importance values for *Acropora palmata*.

Variable	*Percent Contribution*	*Permutation Importance*
Water depth	53.8	62.9
Habitat type	20.9	2.6
Mean summer salinity	16.8	0
Mean summer temperature	6.4	33.5
Slope-of-slope	0.7	0.4
Cosine aspect	0.6	0.4
Slope	0.5	0.1
Sin aspect	0.3	0.2

Discussion

Habitat Suitability Modeling of *A. palmata* in St. Croix

Habitat suitability models for *A. palmata* provided insight into the geographical distribution and some of the potential ecological drivers of this critically endangered species around St. Croix. *Acropora palmata* is a species of great socioeconomic and ecological importance on Caribbean reefs given its contribution to biodiversity, coastal protection, recreation, and tourism (van Zanten et al. 2014). As a major reef-building species, the large and complex structural complexity provides high-quality habitat to many reef fish species, generating the characteristic fish diversity of Caribbean coral reefs (Williams et al. 2017). In St. Croix, some stands of *A. palmata* remain in good health, but many colonies have become degraded or have been lost in the past 50 years due to a combination of disease, marine heatwaves, poor water quality, hurricanes, and extreme swell events (Aronson & Precht 2001; Miller et al. 2009). Many of the most highly suitable sites for this species were found along the reefs of the island's north coast and around Buck Island Reef National Monument where restoration projects in St. Croix have been focused. However, the results of the MaxEnt model also illustrate that suitable habitat for *A. palmata* is not limited to the north coast of the island, where both occurrence sampling efforts and restoration projects have concentrated.

For instance, several highly suitable reefs could be evaluated as potential *A. palmata* outplanting sites along the southeast, north, and west coasts of St. Croix., The majority of historical coral restoration projects have been located along the northeast coast of St. Croix because of the proximity of this area to both existing stands of Acroporid corals, the existence of MPAs, favorable prevailing weather patterns, and physical logistics related to accessibility by boat. This enables restoration projects to be far more practical and cost-effective when plans are realized, given that movements of people, equipment, and ecological resources during the restoration and future monitoring stages are only necessary over much shorter distances. Other unmeasured factors may reduce suitability. For example, Lime Tree Bay on the south coast of St. Croix is highly disturbed by shipping traffic and pollution from the nearby industry. However, if stressors are mitigated at these south coast sites, the potential for outplanting can be evaluated. Of the planned sites, the low percentage of suitable area at Sweepers Complex might have been expected given that this area was selected for its accessibility as an easily accessible 'outreach site' rather than as one of the highest priority outplanting sites (Henderson 2022, personal communication).

Table 3. Area of predicted highly suitable *Acropora palmata* habitat within St. Croix marine protected areas.

MPA	*MPA Type*	*Marine Area* (km^2)	*Area of Highly Suitable* A. palmata *habitat* (km^2)
St. Croix East End Marine Park	Multiple use with no-take zones	149.50	6.54
Buck Island Reef National Monument	No-take & restricted anchoring	76.84	6.58
Salt River Bay National Historic Park and Ecological Preserve	Fishing and boating regulations	4.15	0.12
Mutton Snapper Spawning Aggregation Area	Seasonal closure to fishing	8.81	<0.0001
Red Hind Spawning Aggregation Area East of St. Croix	Seasonal closure to fishing	11.64	<0.001
Total		250.95	13.24

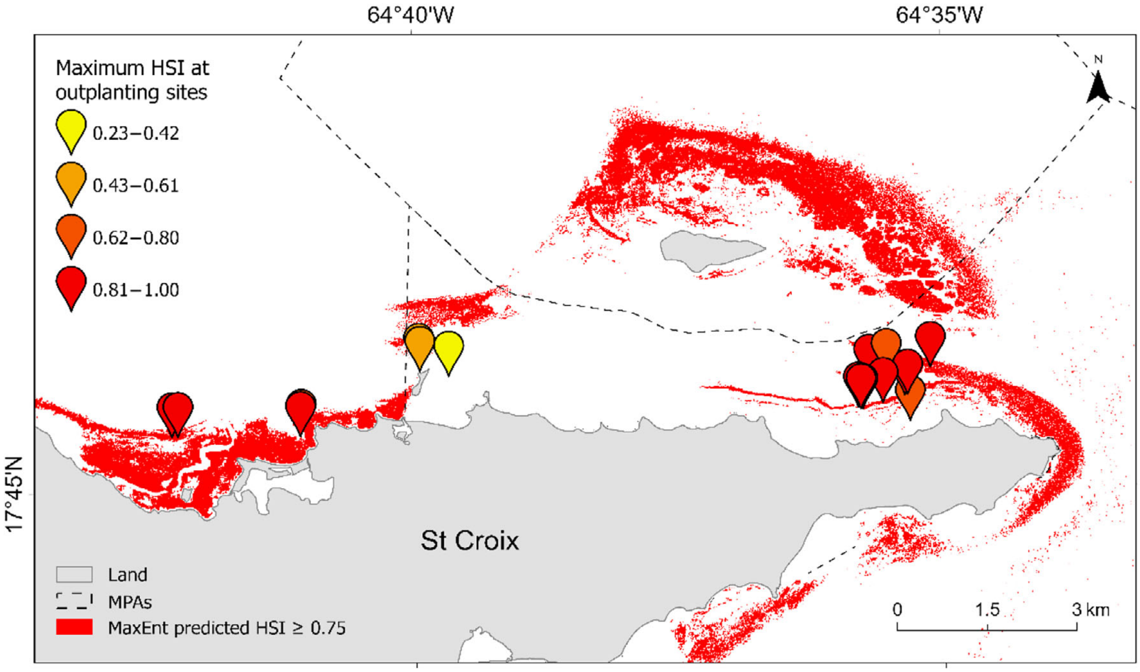

Figure 6. Map showing locations of *Acropora palmata* outplanting sites on St. Croix (U.S. Virgin Islands) showing the MaxEnt habitat suitability index values (maximum) extracted within 30-m radius buffers around each point.

Spatial Predictors Driving *A. palmata* Models

As reported by Wirt et al. (2015), water depth was by far the most important explanatory variable in the constructions of the *A. palmata* models. Bathymetry and its derivative seascape metrics provided great potential alone to generate valuable predictions of habitat suitability. The response curve of *A. palmata* in relation to depth reflected the expected depth range with an optimal depth of around 5 m (Jaap et al. 1989). Mapped benthic habitat types also contributed to the most suitable habitats for *A. palmata* occurring within shallow fore reef and spur and groove geomorphical zones.

The relationship between mean summer temperature and habitat suitability likely reflected the low tolerance of *A. palmata* to temperatures above 29°C. The low contribution of sea temperature and salinity as predictors in this model do not imply that these variables should be discounted as drivers but probably indicate a scale-dependence in the relationship with *A. palmata* and a potential mismatch between the temporal and spatial resolution of the data and the study. The absence of any major rivers on St. Croix also narrows the variability of salinity experienced by corals. Scale-dependency in seascape ecology studies has been highlighted (Wedding & Friedlander 2008; Wedding et al. 2019) and explored in multiscale studies (e.g., Pittman & Brown 2011) that have found different variables to have varying significance as ecological controls at different spatial scales (Pittman et al. 2021).

There are numerous advantages to using a predictive mapping approach and machine learning compared to only using in situ survey-based data to inform restoration site selection. Using MaxEnt, this study rapidly predicted and mapped a habitat suitability index across a broad geographical extent at relatively fine spatial resolution using widely available environmental predictors as spatial proxies. For the marine realm in particular, this approach offers significant benefits given that diver surveys and other in situ data collection approaches are relatively limited in spatial extent, involve some human risk, and can be highly expensive,

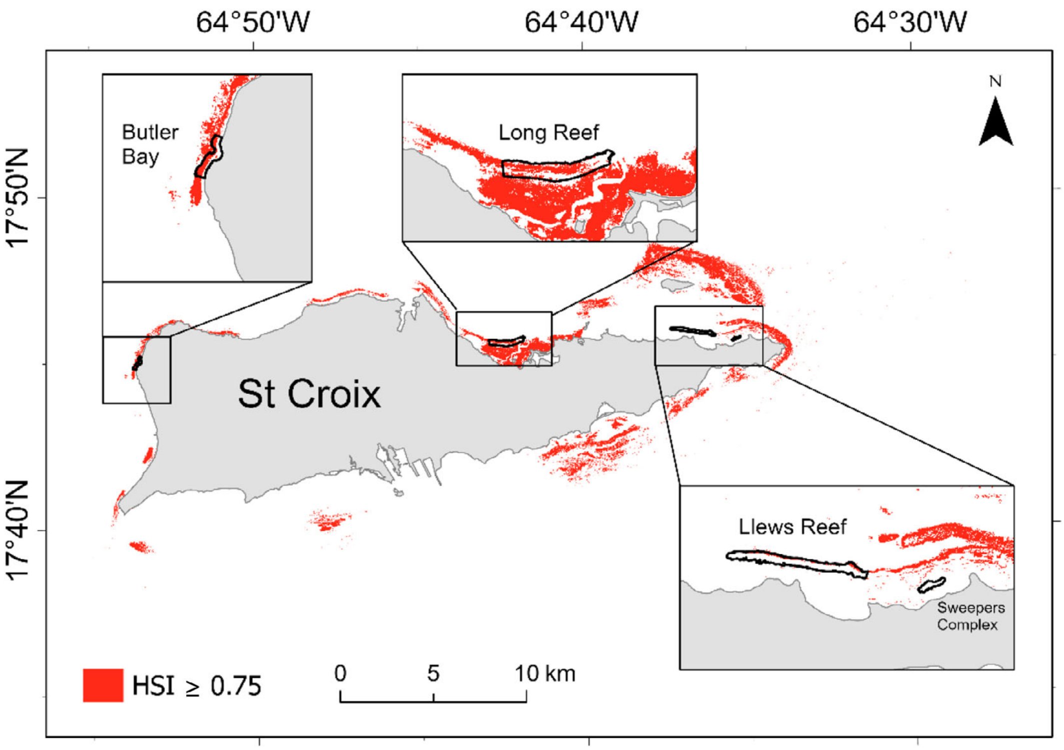

Figure 7. Predicted distribution of high suitability habitat for *Acropora palmata* and the location of four planned outplanting sites around St. Croix, U.S. Virgin Islands. High habitat suitability index (HSI) scores greater than or equal to 0.75 as predicted by MaxEnt.

Table 4. The amount of predicted high habitat suitability for *Acropora palmata* within four planned outplanting sites in St. Croix, U.S. Virgin Islands. High suitability areas have HSI values >0.75.

Outplant Site	*Total Area (m^2)*	*Highly Suitable Area (m^2)*	*% High Suitability*
Long Reef	524,247	250,700	47.8%
Sweepers Complex	47,074	200	0.4%
Llews Reef	366,671	88,400	24.1%
Butler Bay	126,613	69,000	54.5%
Total	1,064,605	408,300	38.4%

time-consuming, and require high levels of expertise. Furthermore, the strong performance of the *A. palmata* model based on its high AUC value shows that modeling approaches such as MaxEnt are viable at the relatively fine spatial scales required for endeavors such as restoration site selection. As both machine learning algorithms and modeling parameterization refinement and data coverage and quality continue to improve, the possibilities for management applications with these methodologies will increase and diversify (Melo-Merino et al. 2020).

Habitat Suitability Modeling Assumptions and Data Limitations

As with any model, certain variables and factors were omitted from consideration, which affected the extent to which the model runs could represent environmental realism (Oreskes et al. 1994). The result was that the model was strongly influenced by water depth but was relatively poor at distinguishing differential habitat suitability at sites of equal and similar depth. In particular, water quality data such as nutrient concentrations and pollutants would have been highly valuable to this study, but the cost and feasibility of collecting these data at the required scales and resolution remain prohibitive. Further, the performance of the marine environmental variables and model inputs are influenced by the spatial, thematic, and temporal scales of the original data (Wedding et al. 2011). Our topographic complexity layer, for instance, was a second-derivative from satellite-derived bathymetry (10 m resolution Sentinel-2 data), which cannot capture the fine-scale complexity that characterizes coral reefs. This is an important consideration as the ecological relationships and key findings could be driven by the source data and spatial scale of analysis (Wedding et al. 2019).

As corals become further threatened by a range of stressors, the species occurrence data upon which models such as MaxEnt can construct statistical relationships dwindles, possibly restricting the usefulness of such an approach. Some of the highly suitable habitat may be relic habitat where *A. palmata* once occurred and where conditions suitable for growth and survival could be restored through threat mitigation—integrating data for the survival of outplants will therefore be a valuable addition to our modeling approach to identify such sites and inform subsequent models once these monitoring data become available. Spatial models can help to identify fragmentation in species distributional patterns and locations to place restoration actions that help bridge gaps in ecological connectivity when scaling up regionally (Kuffner et al. 2020). In the terrestrial realm, human use patterns and land-based sources of pollution also play an important role in habitat suitability, and spatial data layers representing stressors could be integrated as predictors to improve model outcomes. It is essential that those in charge of coral reef restoration projects are as well-equipped as possible to carry out site selection, and habitat suitability modeling may provide one approach alongside many to optimize this process.

Applying Habitat Suitability Modeling to Inform Spatial Prioritization of Reef Restoration

There are several key implications when evaluating the applicability of habitat suitability modeling approaches to coral reef restoration site selection. In most cases, habitat suitability modeling may provide a first step in the site selection process, identifying potential sites that require further examination through either remote sensing or diver-based surveys at very fine scales. Further studies must attempt to incorporate other relevant information necessary for restoration success into comprehensive decision-support tools, including logistics of access, proximity to coral nurseries, ecological connectivity, and known threats from land such as turbidity, nutrients, and toxic contaminants.

Our analyses of both existing and planned restoration sites using the MaxEnt model predictions in this study also demonstrate how such a model may be incorporated into an iterative site selection process alongside existing techniques. While expert knowledge and deliberation will remain essential components of outplant site selection, maps of habitat suitability such as the one produced in this study can offer useful points of information to both guide and review this process. While the majority of existing and planned outplant sites in St. Croix exhibited high levels of habitat suitability according to our model, this method also allowed for critical evaluation of planned restoration sites. For example, the site at Sweepers Complex on the east side of the island exhibited just 0.4% (200 m^2) highly suitable area due to the high coverage of nonsuitable benthic habitat here, while our model revealed several potential sites elsewhere on the island that have not yet been targeted for restoration.

As modeling techniques continue to develop and expand, new analytical approaches will emerge to complement the predictive modeling provided by MaxEnt and similar techniques. Pittman et al. (2018) emphasize the importance of multimodel approaches when using technological techniques in marine ecosystem management. A multimodel approach refers to the implementation of a range of models that can simulate various processes, feedbacks, thresholds, and responses to better capture the complexity of ecosystems in reality. While MaxEnt models may offer useful and insightful information as shown in this study with *A. palmata*, combining the contributions of multiple models in future work may provide a more comprehensive foundation upon which to make decisions regarding restoration strategy. Furthermore, incorporating ecological processes into habitat suitability models, such as hydrodynamic patterns, ecological connectivity, predator distributions and nutrient pathways may help to refine single-species model results (Yates et al. 2018). For example, a multimodel approach to ecological processes has already been successfully applied in the marine literature including dispersal (Kinlan & Gaines 2003), competition (Amarasekare 2008), and ontogenetic shifts (Dahlgren & Eggleston 2000). Integration of in situ data on growth and survival can help link habitat suitability models to key ecological processes. Models that predict ecological connectivity across seascapes for species that influence restoration outcomes can help to build up a more detailed set of ecological scenarios, especially given the importance of sexual reproduction and recruitment for the recovery of resilient communities (Stuart et al. 2021). The combination of a variety of these modeling strategies should facilitate the development of more comprehensive species distribution models that produce more consistently reliable results for managers and policy makers.

Reflecting on Habitat Suitability Modeling Within a Broader Coral Reef Restoration Suite of Approaches

Habitat suitability modeling approaches such as the one employed in this study should be seen to be just one component of a suite of possible tools at ecologists' and policy makers' disposal in the process of site selection for ecological restoration. For some situations, for example, where species distribution gaps present a challenge to site selection, then habitat suitability modeling may play a leading role in guiding site selection in restoration decision-making, and in others, it may be almost entirely insufficient or carry too much uncertainty to inform effective site selection. This study has illustrated that although predictive distribution modeling techniques can offer ecological insight and operationally useful spatial information to support restoration strategies, these modeling approaches may also require refinement and should be tested for their transferability to other regions if they are to be widely applicable as decision-making tools.

This study has aimed to illustrate and evaluate the potential of using predictive habitat suitability modeling to inform coral restoration efforts at a range of spatial scales, from individual coral reefs to restoration planning units to the insular shelf of an island. Our study advances progress in species distribution modeling by providing new insights into the interacting seascape factors controlling *A. palmata* distributions in St. Croix, along with how this information may be deployed alongside conservation managers on the ground to improve the outplant site selection process. This methodology offers a low-cost, rapid, and comprehensive approach to outline the key information required for restoration in novel environments that can be applied at a range of spatial scales and built to incorporate a wide variety of available data sources. However, the paucity of key ecologically important spatial data for tropical coastal areas remains a significant challenge. Although new remote sensing methods are working to overcome this issue, many of these still require organized data collection projects at small scales, which may be time-consuming and/or expensive (Hedley et al. 2016).

Despite the challenges of the data-driven modeling approach demonstrated here, the results of this work offer promise in applications of outplanting site selection in St. Croix, as well as in future projects relating to reef restoration more broadly. One of the aims of this study was to expand on the work of Wirt et al. (2015) and their identification of critical habitat for Acroporid corals in the Caribbean. The results from the *A. palmata* model illustrate the potential of habitat suitability modeling in identifying suitable habitat and informing conservation planning. Although approaches such as these will never be policy-prescriptive, they provide access to insight that is otherwise difficult to obtain at similar scales through traditional methods such as diver-based surveys. However, without the local experience and knowledge of experts in any restoration setting, models such as these hold little value in themselves, and once sites are identified for restoration, further in-depth research will be required to confirm the suitability of sites and monitoring of outcomes. The role of probabilistic analytical modeling techniques such as MaxEnt may be considered as a first step in this process, highlighting suitable habitats at the scale of an island or reef system. As spatial modeling techniques and predictor data improve with time, they will continue to provide more extensive and reliable ecological insight and serve as a cost-effective tool to inform decision-making in conservation planning. The development of multimodel techniques that can capture the huge complexity of marine ecosystems more effectively is an especially exciting prospect for the restoration of coral reefs. As new data becomes available for marine settings at the finest spatial scales, further studies must take advantage of these with the most sophisticated modeling techniques available in order to support marine restoration projects.

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Habitat suitability modeling assumptions and data limitations.
Figure S1. Pearson's correlation matrix for the environmental predictors used in the MaxEnt model.

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