Niche space of corals along the Florida reef tract

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Abstract

Over the last three decades corals have declined precipitously in the Florida Keys. Their population decline has prompted restoration effort. Yet, little effort has been invested in understanding the contemporary niche spaces of coral species, which could assist in prioritizing conservation habitats. We sought to predict the probability of occurrence of 23 coral species, including the critically endangered Acropora cervicornis, using observations at 985 sites from 2011–2015. We ran boosted regression trees to evaluate the relationship between the presence of these corals and eight potential environmental predictors: (i) bathymetry (m), (ii) mean of daily sea surface temperature (SST) (°C), (iii) variance of SST (°C), (iv) range of SST (°C), (v) chlorophyll-a concentration (mg m⁻³), (vi) turbidity (m⁻¹), (vii) wave energy (kJ m⁻²), and (viii) distance from coast (km). The Marquesas and the lower and upper Florida Keys were predicted to support the most suitable habitats for the 23 coral species examined. A. cervicornis had one of the smallest areas of suitable habitat, which was limited to the lower and upper Florida Keys, the Dry Tortugas, and nearshore Broward-Miami reefs. The best environmental predictors of site occupancy of A. cervicornis were SST range (4–5°C) and turbidity (K₄₉₀ between 0.15–0.25 m⁻¹). Historically A. cervicornis was reported in clear oligotrophic waters, although the present results find the coral species surviving in nearshore turbid conditions. Nearshore, turbid reefs may shade corals during high-temperature events, and therefore nearshore reefs in south Florida may become important refuges for corals as the ocean temperatures continue to increase.

1. Introduction

Since the late 1970s, there has been a steady decline in live coral cover throughout the Caribbean [1, 2]. This decline has included unprecedented mortality of two of the Caribbean’s most historically important reef-building coral species, A. cervicornis and Acropora palmata [1, 3]. Most of the acroporid mortality in the Caribbean was caused by disease and thermal-stress events [4–6]. In 2006 this decline prompted the listing of both acroporids as ‘threatened’ under the U.S. Endangered Species Act [7], and in 2008 they were listed as ‘critically endangered’ on the International Union for Conservation of Nature Red List. Decades after the initial
mortality events, coral populations along the Florida reef tract continue to decline [8–10]. It is therefore critical to quantify the contemporary niche space of coral species as marine diseases become more extensive and destructive [11], and as thermal-stress events become more frequent and intensive [12].

Yet niche space has long been an enigma. Niche theory evolved from Elton’s [13] definition of a species’ place in the biological environment and its relationship to food and predators. Later Gause [14] emphasized the role of competitive interactions among species, and Hutchinson [15] delineated a species’ environmentally-driven fundamental niche from its competitive realized niche. MacArthur and May [16] made the implicit assumption that two species could not coexist indefinitely on the same limiting resource, although Roughgarden [17] subsequently advanced niche theory to include low inter-species interactions in high diversity localities. Similarly, Scheffé and van Nes [18] argued that multiple species can coexist in a given niche, which agrees with Hubbell’s [19] assumption of neutrality. However, for coral reefs, such multi-species neutrality may be only relevant in equatorial, benign habitats [20], with higher latitude coral reefs being more susceptible to major physio-chemical drivers such as temperature and light. Superimposed on such niche concepts are background levels of disturbances from hurricanes, thermal-stress events [21], and disease outbreaks [11].

Most contemporary niche models predict the fundamental niche of a species [22, 15], although some niche models include competitive interactions [23] and mechanistic processes [24]. Past niche models along the Florida reef tract suggested that *A. cervicornis* colonies were most common on shallow reefs where temperature fluctuations were moderate [25, 26]. Recently, D’Antonio et al. [27] showed that *A. cervicornis* colonies were found close to shallow reef ridges, where topography was high. Yet wave energy, irradiance, and water quality also influence the physiology and survival of corals [28–33].

This study predicts the contemporary niche space of 23 coral species, including *A. cervicornis*, along the Florida reef tract. Niche space was quantified regionally using niche models [22], which associate the geographic distribution of species with broad-scale environmental conditions. Niche models combine the geographical space of a species with their theoretical-environmental space. The theoretical-environmental space is used to predict the niche of the species, and then that space is projected back onto geographic space, for which environmental conditions are known [34]. The objective of this study was to highlight geographical localities that are most suitable for the survival of 23 coral species along the Florida reef tract. Along with identifying habitats and regions that should be prioritized for conservation purposes, this work could also help guide restoration efforts, highlighting where the outplanting of nursery-reared coral colonies may have the best chance of survival.

2. Methods

**Study area and biological data**

The Florida reef tract runs parallel to the Florida mainland and along the Florida Keys in the southwest (Fig 1). Data on the presence and absence of *A. cervicornis* and 31 other species [i.e., *A. palmata*, *Agaricia fragilis*, *Agaricia lamarcki*, *Colpophyllia natans*, *Dichocoenia stokesii*, *Diploria labyrinthiformis*, *Eusmilia fastigiata*, *Favia fragum*, *Isophyllia sinuosa*, *Madracis decactis*, *Meandrina meandrites*, *Millepora alcicornis*, *Millepora complanata*, *Montastraea cavernosa*, *Mussa angulosa*, *Mycetophyllia sp.*, *Oculina diffusa*, *Orcibella annularis*, *Orcibella faveolata*, *Orcibella franksi*, *Porites astreoides*, *Porites divaricata*, *Porites furcata*, *Porites portes*, *Pseudodiploria clivosa*, *Pseudodiploria strigosa*, *Siderastrea radians*, *Siderastrea siderea*, *Soleniastra bournoni*, *Stephanocoenia interseta*, *Undaria (Agaricia) agaricites*] were examined along the Florida reef tract using the Florida Reef Resiliency Project (FRRP) monitoring dataset from
2011–2015. Note that the models only predicted niche spaces for 23 of the 32 coral species because nine of the species were reported in less than 10% of the sites, making predictions uncertain. The FRRP data were collected at 1028 sites using 10 m x 1 m (10 m²) belt transect surveys (Fig 1). The niche models were trained on a random subset (80%) of the sites and were tested against the remaining 20% of the sites (Table A in S1 File).

Environmental data. Eight environmental predictors, which have been previously shown to influence coral physiology and survival [35–37], were initially examined for incorporation in the niche model: (i) bathymetry (m), (ii) mean of daily sea surface temperature (SST) (°C),...
Table 1. Environmental data used to produce predictor variables in the niche model. The source resolutions are presented in parentheses. The fifth column indicates whether the variable was used in the niche model (I = included, E = excluded).

| Variable                      | Unit       | Source                                           | Period       | Niche Model |
|-------------------------------|------------|--------------------------------------------------|--------------|-------------|
| Bathymetry                    | m          | NOAA (~100 m)                                    | 2016         | I           |
| Mean daily SST                | °C         | USF Optical Oceanography Laboratory (250 m)      | 2011–2015    | I           |
| Variance of daily SST         | °C         | USF Optical Oceanography Laboratory (250 m)      | 2011–2015    | E           |
| Range SST                     | °C         | USF Optical Oceanography Laboratory (250 m)      | 2011–2015    | I           |
| Chlorophyll-a concentration   | mg m⁻³     | USF Optical Oceanography Laboratory (250 m)      | 2011–2015    | I           |
| Turbidity (K₄⁹₀)              | m⁻¹        | K₄⁹₀ NOAA CoastWatch (250 m)                     | 2013–2015    | I           |
| Modeled mean daily wave energy| kJ m⁻²     | fetchR raster (1 km) Remote Sensing Systems CCMP Wind Vector Analysis Product (0.25°) | 2011–2015    | I           |
| Distance from Coast           | km         | Rworldmap                                        | 2018         | I           |

SST indicates sea surface temperature. Where FWC is the Florida Fish and Wildlife Commission, USF is the University of South Florida, NOAA is the National Oceanic and Atmospheric Administration, and CCMP is Cross-Calibrated Multi-Platform. Note that fetchR [39] and RWorldmap [44] are packages in R [45].

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(iii) variance of SST (°C), (iv) range of SST (°C), (v) chlorophyll-a concentration (mg m⁻³), (vi) turbidity (m⁻¹), (vii) wave energy (kJ m⁻²), and (viii) distance from coast (km) (Table 1). A 1-km resolution depth (m) raster file was developed by Ames [38], which was a combination of satellite data and in-situ field measurements. Daily measurements of SST (°C) and chlorophyll-a concentration (mg m⁻³), collated as raster data, with a 0.25 km resolution, were obtained from the University of Southern Florida’s Optical Oceanography laboratory from 2011–2015 (https://optics.marine.usf.edu/). The average SST (°C) was calculated as the mean of daily SST from 2011–2015. The variance of SST (°C), a measurement of thermal variability, was calculated as the variance of daily SST from 2011–2015. The range of SST was calculated by subtracting the minimum temperature from the maximum temperature at every pixel. The average daily chlorophyll-a concentration was calculated as the mean chlorophyll-a concentration from 2011–2015. Turbidity was quantified by the diffuse light attenuation coefficient K at 490 nm (m⁻¹) from NOAA CoastWatch, averaged daily from 2013–2015. Although pre-2013 K₄⁹₀ imagery exists, it does not include the region of interest and so pre-2013 data were not included in the analysis. Wave energy was calculated using inputs of fetch (i.e., the distance of open ocean over which winds travel unobstructed) calculated using the ‘fetchR’ package in R [39], and daily wind speed and wind direction raster data were obtained from Remote Sensing Solutions [40] from 2011–2015. Wave energy was calculated using equations in Chollett and Mumby [41] adapted from [42], where each cell’s fetch was evaluated in the dominant wind direction. If fetch was less than 38 km, then the seas were considered ‘fetch-limited’, whereas if the fetch was greater than 38 km then the seas were considered ‘fully developed.’ A complete explanation of the wave energy calculations is available in the online S1 File. Distance from coast (km) was calculated at the 1-km resolution using the distance function in the ‘raster’ package [43] and the coastline polygon from the high-resolution map in the package ‘RWorldMap’ [44] in R [45]. For spatial consistency, the final input raster files were resampled to a 1-km resolution and masked to a 1km buffer of the Fish and Wildlife Conservation Unified Florida Reef Tract Map (http://geodata.myfwc.com/datasets/unified-florida-reef-tract-map).

Coral niche model. A niche model was developed initially for 32 coral species along the Florida reef tract at 1028 sites from 2011–2015. However, 9 coral species were found in less than 10% of the sites making those models unstable, therefore the results are not included here in the 23 coral species niche model (Table 2). In addition, because *A. cervicornis* is listed as ‘critically endangered’ and is of special interest in this study, an exception to the 10% rule was
made for this species. *A. palmata* is also of special interest but was only recorded in < 0.5% of the sites (Table 2), which made modeling problematic.

We used boosted regression trees (BRTs) [46] to fit the presence and absence of the coral species data, at 1028 sites, to seven of the eight potential environmental predictors (Table 1, Table A in S1 File). Variance of SST was excluded as a potential environmental predictor because there was a strong positive correlation between variance of SST and range of SST (0.71, Fig A in S1 File). Data for each environmental factor were then extracted for each site. Any sites that did not have values for all 7 environmental factors were removed. Of the 1028 total sites, 43 were removed: 22 sites had no SST data, 20 sites had no turbidity data, and 7 sites

Table 2. *In-situ* presence of coral species at sites (%); the modeled area under the receiver operating curve (AUC), which is a diagnostic for model performance; and the percent suitable habitat area (%) predicted by the niche model along the Florida reef tract using data from 985 sites from 2011–2015.

| Species Name                        | Presence at Sites (%) | AUC  | Suitable Habitat Area (%) |
|-------------------------------------|-----------------------|------|---------------------------|
| *Siderastrea radians*               | 47.67                 | 0.66 | 80.5                      |
| *Siderastrea siderea*               | 89.4                  | 0.75 | 75.57                     |
| *Stephanocoenia intersepta*         | 72.28                 | 0.62 | 65.79                     |
| *Solenastrea bournoni*              | 30.06                 | 0.63 | 61.54                     |
| *Millepora alcicornis*              | 88.52                 | 0.75 | 58.34                     |
| *Porites astreoides*                | 80.93                 | 0.68 | 58.09                     |
| *Pseudodiploria strigosa*           | 30.06                 | 0.64 | 57.97                     |
| *Orbicella faveolata*               | 30.35                 | 0.62 | 56.45                     |
| *Dichocoenia stokesii*              | 59.53                 | 0.69 | 55.48                     |
| *Montastrea cavernosa*              | 64.49                 | 0.69 | 55.45                     |
| *Porites porites*                   | 54.96                 | 0.70 | 54.86                     |
| *Undaria (Agaricia) agaricites*     | 48.15                 | 0.71 | 51.36                     |
| *Diploria labyrinthiformis*         | 19.84                 | 0.61 | 49.88                     |
| *Eusmilia fastigiata*               | 16.44                 | 0.59 | 48.73                     |
| *Pseudodiploria clivosa*            | 16.05                 | 0.56 | 46.77                     |
| *Colphophyllia natans*              | 26.65                 | 0.69 | 46.33                     |
| *Porites furcata*                   | 12.55                 | 0.65 | 46.17                     |
| *Porites divaricata*                | 15.08                 | 0.57 | 44.7                      |
| *Orbicella franksi*                 | 12.26                 | 0.74 | 36.34                     |
| *Mycetophyllia sp.*                 | 10.31                 | 0.83 | 32.65                     |
| *Acropora cervicornis*              | 7.78                  | 0.69 | 24.2                      |
| *Meandrina meandrites*              | 31.52                 | 0.57 | 24.12                     |
| *Madracis decactis*                 | 11.28                 | 0.65 | 22.87                     |
| *Agaricia fragilis*                 | 1.75                  | -    | -                         |
| *Agaricia lamarcki*                 | 8.46                  | -    | -                         |
| *Favia fragum*                      | 4.28                  | -    | -                         |
| *Isophyllia sinuosa*                | 0.88                  | -    | -                         |
| *Millepora complanate*              | 2.72                  | -    | -                         |
| *Orbicella annularis*               | 8.95                  | -    | -                         |
| *Mussa angulosa*                    | 3.5                   | -    | -                         |
| *Oculina diffusa*                   | 2.04                  | -    | -                         |
| *Acropora palmata*                  | 0.39                  | -    | -                         |

Where

* indicates coral species that were not present at >10% of the survey sites and were therefore excluded from the model.

** indicates an exception for the 10% rule, because the critically endangered *A. cervicornis* was a species of special interest in this study. The dashes indicate that the coral species were found in less than 10% of the sites, therefore the results are not included.

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had no wave energy data (6 of which also had no SST data). In total, 985 sites were used in the analysis (Fig 1).

We used k-fold partitioning to randomly divide the data into five sections. We used data from four of those sections (i.e., 80% of the data) to train the model and data from one of the sections (i.e., 20%) to test the model. We used a machine-learning algorithm in the form of BRTs to evaluate the relationship between the presence of each species and potential environmental predictors. BRTs fit data by recursively adding ‘trees’ (n-branching nodes) at each iteration—bagged trees take a new bootstrap sample from the training data and choose the next tree that minimizes the ‘loss’ function. We set the bag fraction to 0.8 to introduce some stochasticity into the niche model, which indicates that 80% of the training data were used to fit each individual tree. Additionally, we weighted all sites to generate an equal weight of presences and absences [47]. We built the model using the 'gbm' R package [46] and code adapted from [48]. The niche model was set to a tree complexity dependent on number of environmental factors being tested, a learning rate of 0.0015, and an initial condition of 30 trees.

A 1-km buffer of the coral-reef polygons, found within Florida Fish and Wildlife Conservation Commission-Fish and Wildlife Research Institute’s Unified Florida Reef Tract spatial layer, was used to clip the geographical extent of the model results (Fig 1). The amount of suitable habitat was then calculated as the combined area of cells (km$^2$), above a 50% threshold value. The stepwise iteration process of the BRTs cross-validates at each iteration using data that were not in the immediate bootstrapped training set. The model was run multiple times using different environmental combinations, based on their performance in previous runs, to optimize the model (i.e., the best area under the receiver operating curve) and remove unpredictable environmental variables. The model was then tested for accuracy against the remaining 20% of the dataset, to produce diagnostics of model performance which included constructing confusion matrices (Tables B and C in S4 File). Confusion matrices were computed using the ‘caret’ package [49] in R [45].

We were also interested in the effects of disturbances on the niche space of Acropora cervicornis. Several disturbances occurred either side of our field-sampling window (2011–2015), including a major cold-snap in 2010 [5], Hurricane Irma in 2017, and a disease outbreak (stony-coral-tissue-loss disease) in 2016. Therefore, we took a landscape-metrics approach to simulate the influence of a ‘generic’ disturbance on the predicted patch attributes of Acropora cervicornis along the Florida reef tract. Because Acropora cervicornis colonies are spread across the Florida reef tract as viable patches of subpopulations, disturbances are likely to remove viable patches from the metapopulation, increasing the average distance among the patches. To test this concept and calculate the relative distances between predicted patches of Acropora cervicornis subpopulations on modern reefs along the Florida reef tract, we computed the Euclidean nearest-neighbor distance among the predicted niche patches to examine the average distances between the patches using a series of probability-of-occurrence thresholds. These thresholds simulate different intensities of disturbance, with increasing values simulating increasing intensities of disturbance. All data and R code are available at https://github.com/rvanwoesik/Florida-Niche, and kmz (Google Earth) files of the predicted probability of occurrence of each coral species is available in S4 File.

**Ethics statement**

The field data were collected by participants in the Florida Reef Resilience Program Disturbance Response Monitoring (DRM) https://myfwc.com/research/habitat/coral/drm/. Permission to visit the study sites was granted by the Florida Fish and Wildlife Conservation
Commission and the National Oceanic and Atmospheric Administration. The field studies did not involve the collection of endangered or protected species.

3. Results

Probability of occurrence

The niche model was run on 23 coral species (Table 2). The coral species *Siderastrea radians* and *S. siderea* were predicted to have the largest area of suitable habitat along the Florida reef tract (Table 2, Table 3). *S. intersepta*, *S. bournoni*, *M. alcicornis*, *P. astreoides*, and *P. strigosa* were also predicted to have large areas of suitable habitat, whereas *A. cervicornis* was among the species with the smallest area of suitable habitat along the Florida reef tract (Table 2, Table 3).

The Marquesas, the lower Florida Keys, and the upper Florida Keys were predicted to support the most suitable habitats for the coral species examined (Table 3, Table D in S4 File). The subregions north of Deerfield were predicted to support the lowest suitable habitats for most of the coral species examined, although the more northern habitats had a high probability of occurrence for *M. cavernosa*, *M. decactis*, *M. meandrites*, *M. alcicornis*, and *S. intersepta* (Table 3, Table D in S4 File). For illustrative purposes (Fig 2) we focus on 4 contrasting coral species: *A. cervicornis*, *Mycetophyllia* sp., *O. franksi*, and *S. siderea*, although maps showing the predicted probability of occurrences of all 23 coral species are presented in the online supporting document (Figs B–X in S1–S4 Files). The geographical subregions with the highest probability of occurrence of the critically endangered species *Acropora cervicornis* included the lower Florida Keys (195 km$^2$), the Dry Tortugas (156 km$^2$), the upper Florida Keys (112 km$^2$), and nearshore Broward-Miami reefs (Table 3, Fig 2). The probability of occurrence was lower at Deerfield to South Palm Beach, and the reefs north of South Palm Beach were predicted as unsuitable for *Acropora cervicornis* at the time of surveys (Table 3, Fig 2). *Mycetophyllia* sp. was predicted to occur from the Dry Tortugas through to the middle Florida Keys, whereas the probability of occurrence of *O. franksi* was more restricted, and only included the upper Florida Keys and Biscayne. *S. siderea* had a wide geographic extent and had a particularly high probability of occurrence from the Dry Tortugas through to Miami (Fig 2, Table 3).

Environmental predictors

Distance from the coast, range of SST, bathymetry, and wave energy were the 4 most consistent predictors of the 23 coral species examined (Table 4). Again, for illustrative purposes, we focus on four contrasting coral species (*A. cervicornis*, *Mycetophyllia* sp., *O. franksi*, and *S. siderea*) (Fig 3), although the partial dependency plots that outline the best environmental predictors of the 23 coral species are presented in the online supporting document (Figs B–X in S1–S4 Files).

The best environmental predictors of site occupancy of *A. cervicornis* were SST, moderate turbidity ($K_{000} 0.15–0.25$ m$^{-1}$), and moderate wave energy (>0.5–1.5 kJ m$^{-2}$) (Table 4, Fig 3). The probability of occurrence of *A. cervicornis* was lower where wave energy was > 1.5 kJ m$^{-2}$ (Table 4, Fig 3). *Mycetophyllia* sp., had the highest probability of occurrence when the temperature range was between 4–6˚C, the bathymetry was deeper than 5 m, the chlorophyll-a concentrations were below 1.5 mg m$^{-3}$, and the mean SST was 24˚C (Table 4, Fig 3). The highest probability of occurrence for *O. franksi* occurred in the Dry Tortugas, > 60 km from shore, where wave energy was relatively high (1.2–1.5 kJ m$^{-2}$), and where mean SST was around 25 ˚C (Table 4, Fig 3). Note the flat line in Fig 3B represents a lack of sampling sites between 10 km and 70 km from shore. *S. siderea* had the highest probability of occurrence in habitats that
had low chlorophyll-a concentrations (< 0.3 mg m\(^{-3}\)), mean SST around 26 °C, and wave energy between 1.2–1.5 kJ m\(^{-2}\) (Table 4, Fig 3).

4. Discussion

In the last four decades the Florida reef tract has lost a significant proportion of coral populations, particularly the reef-building corals *Orbicella* and *Acropora* species [1, 2, 50]. The niche models predicted that 13 species of coral were likely to have favorable habitats from the Dry Tortugas to Miami. These species included: *D. stokesii*, *D. labyrinthiformis*, *E. fastigiata*, *M. alcicornis*, *O. faveolata*, *P. astreoides*, *P. divaricata*, *P. furcata*, *P. clivosa*, *S. radians*, *S. siderea*, *S. bournoni*, *S. intersepta* (S3 File for Google Earth kmz files). Seven coral species appeared more sensitive to the environmental variables examined, and their probability of occurrence was

| Coral species          | North Palm Beach | South Palm Beach | Deerfield Broward-Miami | Biscayne | Upper Keys | Middle Keys | Lower Keys | Marquesas Dry Tortugas | Total Area (km\(^2\)) |
|------------------------|------------------|------------------|-------------------------|----------|------------|-------------|------------|------------------------|------------------------|
| *Siderastrea radians*  | 0                | 0                | 0                       | 0        | 328        | 407         | 335        | 404                    | 588                    | 270                    | 2332                   |
| *Siderastrea siderea*  | 13               | 10               | 8                       | 97       | 256        | 347         | 286        | 385                    | 536                    | 233                    | 2171                   |
| *Stephanocoenia intersepta* | 25             | 46               | 17                      | 110      | 130        | 181         | 255        | 419                    | 494                    | 229                    | 1906                   |
| *Solenastrea bournoni* | 1                | 18               | 11                      | 138      | 240        | 361         | 301        | 419                    | 277                    | 2                      | 1768                   |
| *Porites astreoides*   | 2                | 0                | 23                      | 166      | 163        | 220         | 328        | 520                    | 261                    | 1683                   |
| *Pseudodiploria strigosa* | 0              | 0                | 0                       | 146      | 207        | 257         | 382        | 434                    | 254                    | 1680                   |
| *Millepora alcicornis* | 17               | 44               | 15                      | 67       | 220        | 276         | 222        | 344                    | 201                    | 270                    | 1676                   |
| *Orbicella faveolata*  | 0                | 0                | 0                       | 140      | 258        | 196         | 369        | 466                    | 207                    | 1636                   |
| *Dichocoenia stokesii* | 0                | 0                | 0                       | 1        | 204        | 362         | 283        | 405                    | 339                    | 0                      | 1594                   |
| *Montastraea cavernosa* | 31              | 49               | 17                      | 96       | 105        | 81          | 178        | 356                    | 427                    | 253                    | 1593                   |
| *Porites porites*      | 0                | 0                | 0                       | 116      | 268        | 217         | 284        | 421                    | 270                    | 1576                   |
| *Undaria (Agaricia)*   | 0                | 0                | 0                       | 158      | 206        | 213         | 235        | 454                    | 222                    | 1488                   |
| *Diploria labyrinthiformis* | 0            | 0                | 0                       | 118      | 220        | 200         | 297        | 369                    | 241                    | 1445                   |
| *Eusmilia fastigiata*  | 0                | 0                | 0                       | 110      | 172        | 225         | 324        | 367                    | 202                    | 1400                   |
| *Pseudodiploria clivosa* | 0              | 4                | 4                       | 17       | 198        | 264         | 193        | 285                    | 246                    | 1444                   |
| *Porites furcata*      | 0                | 0                | 0                       | 210      | 208        | 245         | 160        | 312                    | 203                    | 1338                   |
| *Colpophyllia natans*  | 0                | 0                | 0                       | 48       | 108        | 187         | 337        | 425                    | 226                    | 1331                   |
| *Porites divaricata*   | 0                | 0                | 0                       | 188      | 265        | 306         | 346        | 110                    | 80                     | 1295                   |
| *Orbicella franki*     | 0                | 0                | 0                       | 105      | 147        | 35          | 54          | 456                    | 256                    | 1053                   |
| *Myctophyllia sp.*     | 0                | 5                | 5                       | 4        | 2          | 6           | 100        | 226                    | 367                    | 237                    | 952                    |
| *Acropora cervicornis* | 0                | 9                | 8                       | 91       | 49         | 112         | 22         | 195                    | 59                     | 156                    | 701                    |
| *Meadrina meandrites*  | 30               | 52               | 19                      | 76       | 27         | 18          | 63          | 123                    | 122                    | 163                    | 693                    |
| *Madracis decactis*    | 29               | 47               | 16                      | 44       | 2          | 8           | 2           | 33                     | 298                    | 188                    | 667                    |
| *Model extent (km\(^2\))* | 33          | 84              | 43                      | 203      | 349        | 433         | 372        | 522                    | 588                    | 270                    | 2897                   |
| **Average**            | **7.54**         | **15.33**        | **6.79**                 | **40.29**| **150.63** | **211.58**  | **204.71** | **301.33**             | **369.83**             | **201.54**             |
| **Rank**               | **9**            | **8**            | **10**                   | **7**    | **6**       | **3**       | **4**       | **2**                  | **1**                  | **5**                  |

The coral species are ranked according to their total area of suitable habitat space (km\(^2\))—depicted in the right-hand column of the table. The subregions are ranked in the last row of the table according to total area (km\(^2\)) of predicted probability of occurrence.

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had low chlorophyll-a concentrations (< 0.3 mg m\(^3\)), mean SST around 26 °C, and wave energy between 1.2–1.5 kJ m\(^{-2}\) (Table 4, Fig 3).

4. Discussion

In the last four decades the Florida reef tract has lost a significant proportion of coral populations, particularly the reef-building corals *Orbicella* and *Acropora* species [1, 2, 50]. The niche models predicted that 13 species of coral were likely to have favorable habitats from the Dry Tortugas to Miami. These species included: *D. stokesii*, *D. labyrinthiformis*, *E. fastigiata*, *M. alcicornis*, *O. faveolata*, *P. astreoides*, *P. divaricata*, *P. furcata*, *P. clivosa*, *S. radians*, *S. siderea*, *S. bournoni*, *S. intersepta* (S3 File for Google Earth kmz files). Seven coral species appeared more sensitive to the environmental variables examined, and their probability of occurrence was
These species included *Acropora cervicornis*, *C. natans*, *M. decactis*, *M. meandrites*, *M. cavernosa*, *Mycetophyllia* sp., and *O. franksi*. For example, the niche model showed that the lower and upper Florida Keys, the Dry Tortugas, and nearshore Broward-Miami County reefs were likely to support *A. cervicornis*, but the middle Florida Keys was less likely to support this species. Similarly, the reef-building coral *O. faveolata* was predicted to favor the habitats in the upper and lower Florida Keys rather than the middle Florida Keys (Table 3). Ginsburg and Shinn [51] first reported on the negative influence of Florida Bay on the middle Florida Keys, and recently Toth et al. [52] showed that reef accretion terminated significantly earlier in the middle Florida Keys than elsewhere, which they suggested was most likely because of negative influences from Florida Bay. It is likely that Florida Bay will continue to influence reefs in the middle Florida Keys, which may prove a disadvantage for many coral species along those reefs.

![Maps showing the probability of occurrence of various coral species along the Florida reef tract](https://doi.org/10.1371/journal.pone.0231104.g002)

Fig 2. The probability of occurrence of (a) *A. cervicornis*, (b) *Mycetophyllia* sp., (c) *O. franksi*, and (d) *S. siderea* along the Florida reef tract based on the niche model calculated using boosted regression trees using data from 985 sites from 2011–2015.
The best environmental predictors of site occupancy of the ‘critically endangered’ *A. cervicornis* were moderate turbidity, SST, and wave energy. Although historically *Acropora* corals are known to survive best in oligotrophic waters [53–55], the present results suggest that on modern reefs, near zero turbidity was not optimal for *A. cervicornis*. Rather, a moderate turbidity value of between 0.15–0.25 m$^{-1}$ showed the highest probability of occurrence. These results agree with physiological studies, which show that reducing light by shading can effectively reduce the influence of temperature anomalies [57–59]. Indeed, thermal-stress events may be shifting the optimal niche space of corals toward more turbid habitats, for example to nearshore reefs of Broward-Miami subregion, as ocean temperatures increase [56].

The 7 predictor variables include: distance from coast (km), range of SST (˚C), bathymetry (m), wave energy (kJ m$^{-2}$), chlorophyll-$a$ concentration (mg m$^{-3}$), mean of daily sea surface temperature (SST) (˚C), and turbidity (m$^{-1}$). Variance of SST (˚C) was excluded as a potential environmental predictor because there was a strong positive correlation between variance of SST and range of SST. Dashes indicate minimal significance of predictive variable.
geographic sampling and mismatches of scale between the organism and environmental covariates. For example, an observed absence of a coral in a 10 m$^2$ belt transect in the field does not necessarily imply a complete absence throughout a 1-km$^2$ grid cell, at which the environmental variables are considered. Therefore, an absence might not be considered a 'true absence' [61] and would reduce the model’s predictive capacity. Secondly, while a dominant species might occupy most of its fundamental niche space, rare species might occupy only a small proportion of their fundamental niche [62]. Dispersion limitation may further prevent the rare species from occupying all the potential niche space, and therefore predicting the probability of occupancy may be over-estimated (i.e., with high false positives).

Since niche models are known to be prevalence-dependent [63], low in-situ occurrences will translate to low accuracies. Indeed, the niche models had high specificity and low sensitivity (see S4 File for full specificity and sensitivity results). Specificity is an indicator of how good the model is at detecting true negatives, whereas sensitivity is an indicator of how good the model is at detecting true positives. In other words, the niche models were good at predicting...
habitats in which a particular species was unlikely to be present, but less accurate at predicting habitats in which a species could occur. This strong specificity and low sensitivity are expected in localities such as the Florida reef tract, where the organisms do not occupy the entire niche space because the system has undergone recent disturbances. Such disturbed environments reflect data that are unbalanced toward absences, although we did compensate for this issue by generating an equal weight of presence and absence sites [47]. The simulations that examined disturbances to the predicted patches of *Acropora cervicornis*, using a series of probability-of-occurrence thresholds, found that patch distances were on average 2–3 km (Fig Y in S4 File) on modern reefs along the Florida reef tract, and that distances between the patches are likely to increase with an increase in disturbances. These results are troublesome considering the fragile nature of the modern metapopulation of *Acropora cervicornis*. The niche models can be improved in the future by hierarchically adding spatial and temporal complexity, although we expect that the general geographic patterns will hold up. The models can also be improved by adding more local information, such as macroalgal cover, since low macroalgae coverage has been shown to increase the survival of *A. cervicornis* [64].

5. Summary and conclusions
Recent changes in environmental conditions along the Florida reef tract may have shifted, and even narrowed, the niche space of some sensitive coral species [8], and consequently information on the distribution of coral species from decades past may no longer provide information for present niche space. Previously, the most optimal purported niche space for *A. cervicornis* was in clear oligotrophic waters, although the present results suggest that turbid conditions are more optimal on modern reefs that frequently experience high heat stress. Therefore, the near-shore reefs along the Florida reef tract may become important refuges for corals as the ocean temperatures continue to increase.

Supporting information
S1 File. (DOCX)
S2 File. (DOCX)
S3 File. (DOCX)
S4 File. (DOCX)
S5 File. (ZIP)

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