

Identifying coral species traits associated with resilience across Florida's Coral Reef.



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Final Report

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June/2025

Completed in Fulfillment of C3EFD9 for

**Florida Department of Environmental Protection
Coral Protection and Restoration Program
8000 N Ocean Dr.
Dania Beach, FL 33004**

**This [report, workshop proceedings, etc.] should be cited as follows:
{Zinman, S., Jones, N. P., Hadj-Hammou, J., Bauman, A. G. 2025. Identifying coral species traits associated with resilience across Florida's Coral. Florida DEP. Dania Beach, FL. 1-30.}**

This report was funded through a contract agreement from the Florida Department of Environmental Protection's (DEP) Coral Protection and Restoration Program. The views, statements, findings, conclusions, and recommendations expressed herein are those of the author(s) and do not necessarily reflect the views of the State of Florida or any of its subagencies.



Acknowledgements

We would like to thank to Dr. Alain Zuur for his assistance with statistical modeling. We would also like to thank Patrick Idank, Bernhard Riegl Junior, and Madison Androne for their assistance in field work. We would also like to thank the Florida Department of Environmental Protection Florida's Coral Reef Resilience Program Grant for funding this project.

Management Summary (300 words or less)

Species traits offer insights into coral resilience and ecosystem functions (e.g., habitat provision, reef growth) in the face of climate change. This project had three goals: (1) examine what the effects of recurrent disturbances (i.e., heat, hurricanes, disease) across time were on coral species traits, trait redundancy, and trait space along Florida's Coral Reef (FCR); (2) assess which coral species traits are resilient to thermal stress (hot/cold), hurricanes, and coral disease; and (3) determine which coral traits are predominant within source and sink reef hotspots and priority restoration sites along FCR. We combined long-term coral monitoring datasets, global trait databases, and spatial disturbance records to address Goals 1 and 2, and conducted *in situ* trait measurements across FCR for Goal 3. Our findings show that Florida's coral communities exhibit low trait diversity and limited variability in trait composition, largely shaped by recurrent heat stress and hurricane impacts. This highlights the need for management to support and enhance trait diversity, as it underpins multiple reef ecosystem functions. Florida-specific trait data found higher trait diversity than available ocean-wide trait data, highlighting the importance of incorporating trait-based approaches into management efforts. Restoration efforts should focus on coral species identified as contributing most to increased trait diversity and resilience—particularly in areas with low existing diversity. We also provide a ranking of coral species based on their trait contributions and resilience, offering a practical tool to guide species selection for restoration and monitoring efforts. Expanding coral monitoring to include species trait measurements will improve long-term management outcomes.

Executive Summary (max 1 page)

Over the last three decades, coral population decline and lack of recovery along Florida's Coral Reef (FCR) from multiple recurrent disturbances has instigated the expanding application of coral restoration and conservation efforts. However, efforts thus far have focused on taxonomic approaches. While taxonomic approaches are important, these approaches may miss crucial changes in other aspects of FCR such as ecosystem functions (e.g., herbivory, habitat provision). Trait-based approaches offer a complimentary method to evaluate coral community reassembly and changes to ecosystem functions and resilience traits under ongoing global change. To address this gap, our aim was to identify coral species traits associated with resilience (defined as the capacity for coral populations to regain their fundamental structure, processes, and functioning following disturbances) to thermal stress and disease along FCR. Specifically, we had three goals: (1) examine what the effects of recurrent acute disturbance events (i.e., thermal, disease) across time were on coral species traits, trait redundancy, and trait space along FCR, (2) assess which coral species traits are resilient to thermal stress (hot and cold) and disease (i.e., SCTLD, black band disease), and (3) determine which coral traits are predominant within source and sink reef hotspots and priority restoration sites along FCR. We used long-term monitoring data from CREMP and SECREMP to analyze coral species abundance, disease prevalence, and sea surface temperature patterns across 79 sites along FCR. Global trait datasets and literature reviews provided species-level trait information, which was combined with resilience metrics using random forest and mixed model analyses to identify traits associated with disturbance resistance. To complement this, field surveys at 23 additional reef sites measured colony-level traits (e.g., corallite width, tissue thickness, growth form, surface complexity) using photogrammetry, image analysis, and microscopy. Kruskal-Wallis tests, principal coordinate analyses, and cluster dendrograms compared trait composition and diversity across regions and restoration priority sites to guide management decisions. We also ranked coral species for restoration efforts to prioritize increasing trait diversity and resilience. Species were assigned an overall score based on individual scores of the presence of resilience traits and their contribution to increasing trait diversity and decreasing trait redundancy. We found Florida's coral communities had low trait diversity, high trait redundancy, and little variation in trait composition. Furthermore, recurrent disturbances (i.e., heat, hurricanes) have driven declines in trait diversity and changes in trait composition. Overall, our findings highlight the need for management to support and enhance trait diversity, as it underpins multiple reef ecosystem functions. Restoration efforts should focus on coral species identified as contributing most to increased trait diversity and resilience—particularly in areas with low existing diversity. We also provide a ranking of coral species based on their contributions to trait diversity and resilience, offering a practical tool to guide species selection for restoration and monitoring efforts. Expanding coral monitoring to include species trait measurements will improve long-term management outcomes.

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1. BACKGROUND/INTRODUCTION: BRIEF SUMMARY OF THE PROJECT AND WHY IT IS NEEDED. INCLUDE A DESCRIPTION OF WHAT WORK WILL BE PERFORMED AND/OR COMPLETED WITH THE DEP FUNDING.

Over the last three decades, coral population decline and lack of recovery along Florida's Coral Reef (FCR) from multiple recurrent disturbances (e.g., coral disease, thermal stress events, and chronic local stressors; Jones et al., 2022; Manzello et al., 2007; Muller et al., 2020) has instigated the expanding application of coral restoration and conservation efforts. In order to manage and restore coral populations along FCR, it is critical to understand the impact of recurrent disturbances on FCR. Recurrent disturbances on FCR have been driving the decline of coral communities. However, susceptibility and mortality in response to recurrent disturbances vary greatly among coral taxa, leading coral communities on FCR to reassemble (Toth et al., 2019). Specifically, this reassembly represents shifts in dominance from reef-building coral species, such as *Acropora palmata* and *Orbicella faveolata*, to smaller weedier species, such as *Porites astreoides* and *Siderastrea siderea* (Toth et al., 2019). This coral community reassembly and shift in dominance may result in a loss of critical ecosystem functions. However, changes to ecosystem functions are often overlooked by studies focusing purely on coral community composition. This means that these studies may overlook critical changes to coral reefs, which would be caught by alternative approaches, such as trait-based approaches (Hughes et al., 2018; McWilliam et al., 2020).

Trait-based approaches are a novel method for evaluating coral community reassembly and changes to ecosystem functions and resilience traits under ongoing global change (Streit and Bellwood, 2023; McWilliam et al., 2020; Mudge and Bruno, 2023). Trait-based approaches examine changes in species traits (i.e., any measurable feature of a species' morphology, behavior, or life history; Streit and Bellwood, 2023) as proxies representing both how species respond to their environment and their roles in ecosystems (Streit and Bellwood, 2023). By understanding changes in individual traits, trait diversity (i.e., the trait differences between organisms present in a community or ecosystem), and trait redundancy (i.e., the number of different species with the same trait value), these approaches link diversity to ecological processes, providing insight into future ecosystem functioning and stability (Green et al., 2022; Madin et al., 2016a; Madin et al., 2016b; McWilliam et al., 2020; Streit and Bellwood, 2023). Species rich ecosystems contain a wide diversity of species traits, and often high redundancy in those traits (McWilliam et al., 2018; Wong et al., 2018). However, disturbances can reduce redundancy, leaving those ecosystems vulnerable to the complete loss of traits, trait diversity, and ecosystem functions.

Trait-based approaches have revealed critical changes in coral populations following disturbance, that are often overlooked by other approaches (e.g., coral cover). For example, after thermal-stress events, coral taxonomic diversity, coral trait diversity, and coral trait redundancy often decline (Hughes et al., 2018; McWilliam et al., 2020; Zawada et al., 2019). However, during the recovery period following disturbance, taxonomic diversity recovers but trait diversity and redundancy often fail to recover (Hughes et al., 2018; McWilliam et al., 2020). Trait-based approaches to coral reefs have also been used to identify extinction risk and resilience to elevated

temperature and acidity through the identification of traits which convey resilience to stress and disturbance (hereafter denoted as resilience traits; Madin et al., 2023; McWilliam et al., 2022). Identifying resilience traits and trait diversity has been used to inform restoration efforts in eastern Australia, using a two-part hedging approach which ranks optimized species for restoration based on the presence of resilience traits and the ability to expand trait diversity to optimize ecosystem functions and services (Madin et al., 2023). However, trait-based approaches have not been applied to FCR or coral restoration efforts in Florida. This project begins to fill this gap in trait-based approaches to FCR and builds on the work of Madin et al. (2023) to develop trait-based priorities in coral restoration efforts. This project is significant because it identifies and clarifies mechanisms of coral decline in the context of stony coral species traits on FCR in order to identify traits associated with resilience and aid restoration efforts in counteracting this decline on FCR by bolstering resilience on FCR.

1.1. Project Goals:

Our research goal was to identify coral species traits associated with resilience (defined as the capacity for coral populations to regain their fundamental structure, processes, and functioning following disturbances) to thermal stress and disease along FCR. Specifically, we had three goals: (1) examine what the effects of recurrent acute disturbance events (i.e., thermal, disease) across time were on coral species traits, trait redundancy, and trait space (i.e., evenness, richness, divergence/dispersion) along FCR, (2) assess which coral species traits are resilient to thermal stress (hot and cold) and disease (i.e., SCTLD, black band disease), and (3) determine which coral traits are predominant within source and sink reef hotspots and priority restoration sites along FCR.

Our primary objectives were:

Objective I (pertains to questions (1) and (2)): Utilize long-term monitoring data and globally averaged stony coral species trait data to determine how recurrent acute disturbance events (i.e., thermal, disease) are affecting coral species traits and trait diversity/redundancy over time and identify resilience traits that persist following recurrent disturbances.

Objective II (pertains to question (3)): Identify species traits in situ to assess whether priority restoration coral species support coral resilience and trait diversity within source and sink hotspots of FCR and priority restoration sites.

2. METHODS

2.1. Objective I

Hard coral percent cover data and the percent abundance of disease for an eleven-year period (2011 to 2022) was extracted from the Coral Reef Evaluation and Monitoring Project (CREMP) and Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP). Any transects with

less than three coral species were removed to focus on interspecific trait variation. The coral species percent cover data was converted to relative abundance and contained 47 species overall. However, 14 species presented difficulties in identification and thus were grouped into five species complexes (see Supplementary Information). These datasets include coral cover data for 57 sites across FCR.

Sea surface temperature (SST) data from January 1, 2011, to December 31, 2022, was downloaded from the National Oceanographic and Atmospheric Administration (NOAA) 0.25-degree Daily Optimum Interpolation Sea Surface Temperature (OISST) Version 2.1 through the NOAA ERDAP data server (R package: RERDDAP; Huang et al., 2020; Chamberlain, 2024; R Core Team, 2023) for every CREMP site. Average monthly mean SST data was collected from the climatology development for NOAA Coral Reef Watch's 5-km product suite for each subregion from 2011 to 2022 (Heron et al., 2014). This data was used to calculate several temperature metrics: maximum yearly SST, minimum yearly SST, Degree Heating Weeks (DHWs), and Degree Cooling Weeks (DCWs). To calculate DHWs and DCWs, DHWs were calculated with the following equation: $DHW_i = \sum_{j=i-83}^i (\frac{HS_j}{7})$, where HS_j is the number of degrees Celsius above the average maximum temperature. DCWs were calculated with the following equation: $DCW_i = \sum_{j=i-83}^i (\frac{CS_j}{7})$, where CS_j is the number of degrees Celsius below the average minimum temperature. Additionally, the number of hurricanes whose path overlapped with FCR, and the average strength of those hurricanes was recorded for each year (2011 to 2022; Knapp and Kossin, 2007).

To examine temporal variation among reef communities along FCR, eight coral traits ([1] reproductive strategy, [2] corallite width minimum, [3] corallite width maximum, [4] growth form, [5] sexual system, [6] bleaching response index, [7] symbiont transmission mode, [8] growth rate) were collected from the coral trait database (www.coraltraits.org; Madin et al, 2016) and literature review. These traits were selected because literature analysis revealed that they are response traits connected to the disturbances evaluated, and many influence life history strategy. Response traits are defined as traits which show how an organism responds to change in the environment (Streit & Bellwood, 2023). These traits were also selected based on data availability. Where applicable, coral species trait data was filtered to global estimates to avoid values specific to regions outside of Florida. For five coral complexes, continuous coral species traits within a given complex were averaged to obtain trait data on the complex level (see Supplementary Information). All coral species traits had at most 40% missing values. Missing trait values were imputed using the rfrImpute function in R programming language version 4.3.1 (package: randomForest; Liaw & Weiner, 2002; R Core Team, 2023), which utilizes a random forest analysis to place trait values based on similarities in trait communities between species and common patterns in trait values. Species trait data was compiled into a 'species × trait' matrix where cells are trait values, rows are coral species, and columns are species traits.

Functional diversity (i.e., functional richness and Rao's quadratic entropy), functional redundancy, and community weighted means (CWMs) were calculated for each year from relative abundance

data and the ‘species $\times$ trait’ matrix (R programming language package: “FD”; Botta-Dukát, 2005; Laliberté & Legendre, 2014; R Core Team, 2023; Villéger et al., 2008). CWMs are calculated as the average trait values in a community, weighted by species’ relative abundance. Functional richness was calculated as the convex hull volume bounded by species within trait space (R programming language package: FD; Laliberté & Legendre, 2014; R Core Team, 2023; Villéger et al. 2008) whereas Rao’s Quadratic Entropy was calculated as the average distance of abundance-weighted maximum pairwise distances in trait space for each community (R package: FD; Laliberté & Legendre, 2014; R Core Team, 2023; Mouillot et al., 2013). Functional redundancy was calculated following Ricotta et al. (2016), where functional redundancy is equal to one minus Rao’s quadratic entropy divided by the Simpson diversity (R packages: “FD” and “vegan”; Laliberté & Legendre, 2014; Oksanen et al., 2022; R Core Team, 2023). Functional richness is not abundance weighted, while Rao’s quadratic entropy and functional redundancy are abundance weighted. This allows for comparisons to evaluate the effects of coral species abundance changes in trait space.

Pearson correlations were run to check for collinearity between disturbance variables (with a cut off value of 0.6) and showed high collinearity between minimum SST and DCWs, and maximum SST and DHWs (see Supplementary Information). To examine the distribution of species within trait space, a Principal Coordinates Analysis (PCoA) was run using Gower distance-adjusted ‘Species $\times$ Trait’ data to standardize traits which have varying scales (R packages: “FD”, “stats”; Laliberté & Legendre, 2014; R Core Team, 2023). The PCoA was converted into a heatmap to visualize the density of species within a given point of trait space, following the methods of (Tebbett et al., 2021). To convert the PCoA to a heatmap, Kernel Utilization Distributions were calculated from the PCoA scores to create heatmaps of trait space for each year (R package: “MASS”; Venables & Ripley, 2002).

Generalized additive mixed effects models (GAMMs; R package: “mgcv”; Pedersen et al., 2019; Wood, 2003; Wood, 2011) were run to determine how disturbance factors (minimum SST, maximum SST, DCWs, DHWs, average hurricane strength, and the percent abundance of disease) drive temporal variation in functional diversity and redundancy metrics over time. GAMMs were chosen because of the lack of normality and lack of homoscedasticity in the data, and because of repeated measures in the permanent transects. To avoid collinearity, six GAMMs were run, with two for functional richness, two for Rao’s quadratic entropy, and two for functional redundancy. The models for functional richness used a gamma distribution with a log link function, while models for functional redundancy and Rao’s quadratic entropy used a beta distribution with a logit link function, as both of those metrics are on a zero to one scale (see Supplementary Information for more detailed GAMM methods). Additional models were run with smoothers on year by habitat, percent abundance of disease, and percent abundance of disease by habitat. The “DHARMA” package in R was used to test model fit and dispersion for each model. The Akaike Information Criterion (AIC) score was calculated for each model and the mode with the lowest AIC was chosen for each diversity/redundancy metric.

Linear regressions was carried out using CWMs to examine what disturbance factors were driving

temporal variation in trait composition (Adonis function; package: vegan; Oksanen et al., 2022). To avoid collinearity, two linear regression models were run. One model used the following equation: Gower distance-adjusted CWMs ~ minimum SST + maximum SST + the number of hurricanes + the average strength of hurricanes + the percent abundance of disease + year. The other model used the following equation: Gower distance-adjusted CWMs ~ DHWs + DCWs + the number of hurricanes + the average strength of hurricanes + the percent abundance of disease + year. To account for the repeated measures of the permanent transects, all the linear regression models were stratified by site.

A redundancy analysis (RDA; Greenacre, 2018) was conducted on the coral species abundance by time, habitat, and disturbance metrics (minimum SST, maximum SST, DCWs, DHWs, average hurricane strength, and the percent abundance of disease; see supplementary information) to build a two-dimensional representation of how species respond to disturbance. A regression tree was built on the first two RDA axes by species traits to determine which traits explain the most variation in species responses to disturbance (R packages: “rpart”; Therneau et al., 2013). A regression tree was chosen to determine what specific trait values were most explaining species response to disturbances and what percent of species had each of those specific trait values. A random forest model based on a cluster dendrogram of the CWMs was run to determine which traits explain the most variation in the trait composition.

2.2. Objective II

2.2.1. Field sampling

This study was conducted at 23 reef sites across the Kristin Jacobs Coral Aquatic Preserve (Coral AP) on or near priority restoration sites and source/sink hotspots (Figure 1). These sites were chosen to be near but not on SECREMP sites, as to expand our range of data across the CORAL AP Haphazard surveys of coral colony traits of the four dominant priority restoration coral species (*Montastrea cavernosa*, *Porites asteroides*, *Siderastrea siderea*, *Stephanocoenia intersepta*) were collected at each site. For each survey, two coral colonies greater than two centimeters for each species were included. The two-centimeter minimum is used to exclude juvenile coral populations and remain consistent with CREMP procedures. This method was chosen in order to maximize our understanding of coral species traits on FCR, particularly for priority restoration species, while following ethical and legal restraints (i.e., endangered species ethics and law). Coral colony health (e.g., bleaching status based on color maps such as the one in this publication [Siebeck-et-al-2006-Monitoring-coral-bleaching.pdf \(coralwatch.org\)](#), disease status: examples of diseased colonies in this link: [Coral Disease Identification - AGRRA](#), predation) and a suite of coral species traits (e.g., growth form, colony area, surface complexity, volume compactness, corallite width, tissue thickness) were recorded for each coral colony.

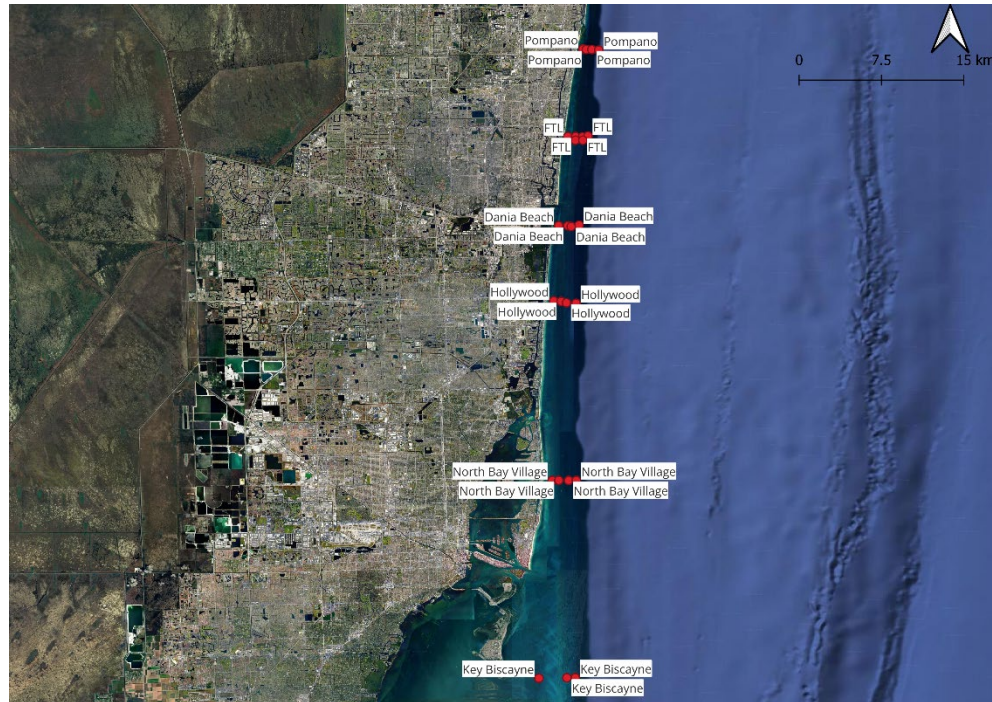


Figure 1: Map of reef sites across the Kristin Jacobs Coral Aquatic Preserve on or near priority restoration sites and source/sink hotspots

2.2.2. Trait measurements

Trait measurements and calculations utilized common procedures from the Coral Trait Database (Madin et al., 2016a), Veron (2000), and Zawada et al. (2019). For each colony, the taxonomic designation to the lowest level, and the growth form derived from the Veron (2000) textual descriptions, were recorded *in situ* and confirmed from images of the colonies upon returning to the laboratory. An image was taken of each colony about 40 centimeters above the substrate with a scale bar as a size reference. The planar area of the colony was measured using ImageJ software (Schneider et al., 2012) upon returning to the laboratory.

Photogrammetry procedures were used to measure surface complexity and volume compactness. Photogrammetry was not possible for particularly short encrusting species. Photogrammetry occurred by taking photographs of the coral colony around every side of the colony and over the top of it. A scale bar was placed around the colony prior to the photographs being taken. Each photograph overlapped in coverage of the coral colony by 80% to allow for the images to be stitched together into 3D image of the coral colony. Upon returning to the lab, the images were stitched together into a 3D model using Agisoft metashape (Agisoft Metashape Professional Edition, 2016). The volume and surface area of each model and the volume and surface area of a convex hull around the model were measured using Meshlab (Cignoni et al., 2008). Convexity, as a measure of volume compactness, was calculated as the model volume

divided by the convex hull volume. Packing, as a measure of surface complexity, was calculated as the model surface area divided by the convex hull surface area.

Corallite width was measured through two methods. For corallites at least 2 mm wide, five corallites on the colony were randomly selected and the distance between opposite ends of the corallite measured with calipers. In the second method, a tissue sample of two corallites was removed from the edge of the colony. This sample was placed in sample bags and stored in ethanol. Upon returning to the laboratory, the distance between opposite ends of each corallite sampled was measured with calipers utilizing a Nikon SMZ-745w 6.7x to 50x zoom microscope. The microscope allows for the accurate measurement of corallite width, regardless of size. In addition to corallite width, the coral samples were used to measure tissue thickness. Tissue thickness, measured in mm, was measured with calipers on cross sections utilizing a Nikon SMZ-745w 6.7x to 50x zoom microscope.

2.2.3. Data analysis

To determine how similar sites, including DEP priority restoration sites, and habitat (i.e., nearshore reef, inner reef, middle reef, outer reef) were from each other cluster dendrograms, and principal coordinates analyses were performed. Due to a lack of normality, Kruskal-Wallis tests where habitat (i.e., nearshore reef, inner reef, middle reef, outer reef) and site are factors were run to assess if trait diversity and redundancy change between habitat, and site, including DEP priority restoration sites.

2.3. Ranking of coral species for restoration

In-situ trait data was used to validate coral species trait data from objective I before all species trait data and abundance data were used to calculate a ranking for restoration species. This ranking followed the same approach as Madin et al. (2023). Coral species were ranked for importance to restoration based on presence/absence of resilience traits and the species' ability to expand trait diversity. This ranking was built from a combination of two scores, one for the number of resilience traits and one for the species ability to expand trait diversity. The resilience score for each species was assigned based on how many of the traits identified as resilient in objective I a given species contains. The score was calculated by assigning three points if the corallite width was less than 14 mm, assigning two points if the growth rate was less than 13 mm/year, and assigning one point if the growth rate was greater than 4.9 mm/year. These specific species trait values and their importance were determined by a regression tree analysis in objective I. Functional dispersion was used to calculate the trait diversity score because functional dispersion is a metric representing how much a given species contributes to expanding trait diversity. The resilience score and trait diversity score were added together to create an overall score from which coral species could be ranked. However, every score was standardized before coral species were ranked based on their resilience and ability to expand trait diversity.

3. RESULTS:

3.1. Objective 1:

3.1.1.1. Patterns in trait space and diversity

There were four small points of densely occupied trait space, where the gradient rapidly drops to no occupation away from those points, however most trait space remained unoccupied (Figure 2). Additionally, the occupied points of trait space did not vary between years in terms of location in trait space or density (Figure 2). The trait spaces revealed that coral communities in FCR contained a few combinations of traits, which appear to be highly redundant.

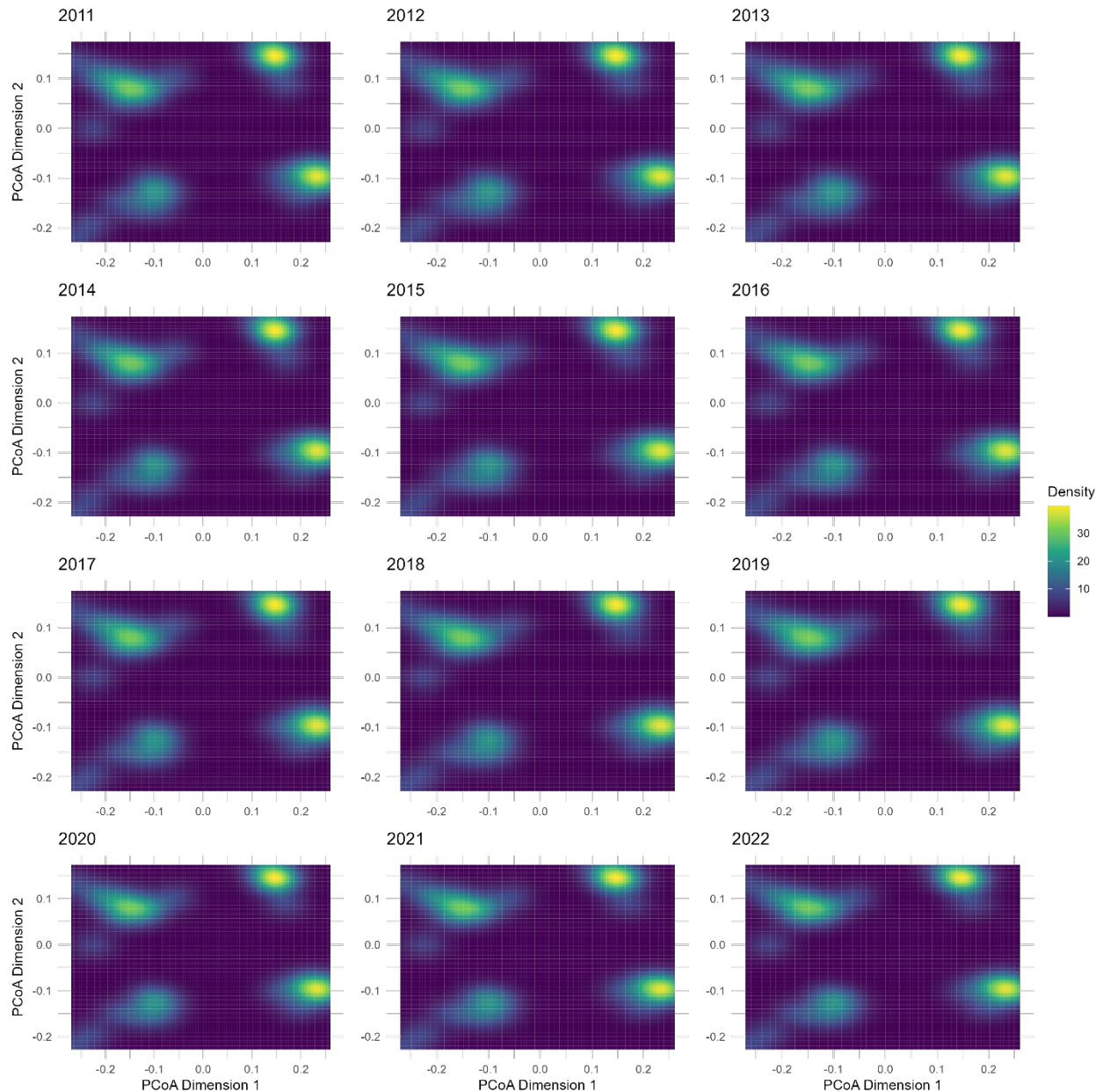


Figure 2: Temporal variation in trait space of the coral community of the entirety of Florida's Coral Reef. The trait spaces for each year represent the multidimensional assemblage of traits.

The density of the occupation of trait space is represented by heat maps based on kernel utilization densities, where yellow represents more organisms with the particular combination of traits represented by a given position of the PCoA, and blue represents less samples with the particular combination of traits represented by a given position of the PCoA.

The coral communities of FCR had very low functional richness (Figure 3A) and Rao's quadratic entropy (Figure 3B) and very high trait redundancy (Figure 3C) throughout the observed time-period. All three trait diversity/redundancy metrics show small temporal variation.

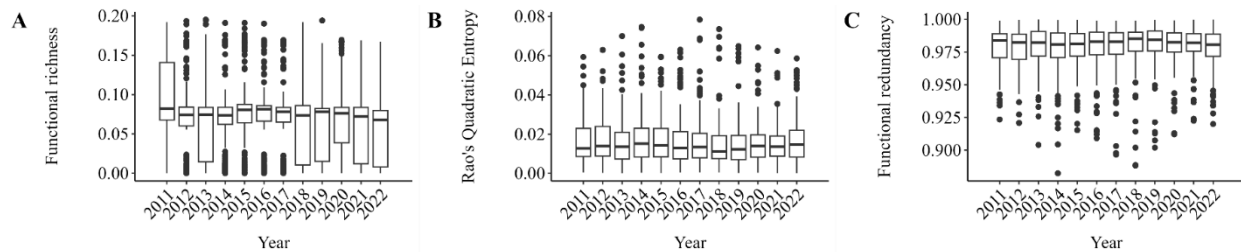


Figure 3: Temporal variation in (A) functional richness, (B) Rao's quadratic entropy, and (C) trait redundancy. Points represent outliers that lay outside the distribution of the boxplots.

3.1.1.2. Temporal patterns in disturbance

Heat stress occurred every year except 2013 and 2014 (Figures 4A and 4B). In contrast, cold stress only occurred in earlier years, specifically 2011, 2014, 2015, 2016, and 2018 (Figure 4A and 4B). However, cold stress was infrequent and decreasing across the timespan (Figures 4A and 4B), with the only major cold stress event occurring in 2011 (Figure 4B). Similarly to heat stress, disease occurred at a consistent level every year (Figure 4C). On the years where hurricanes crossed FCR, there was only one of varying strengths hurricane per year (Figure 4D).

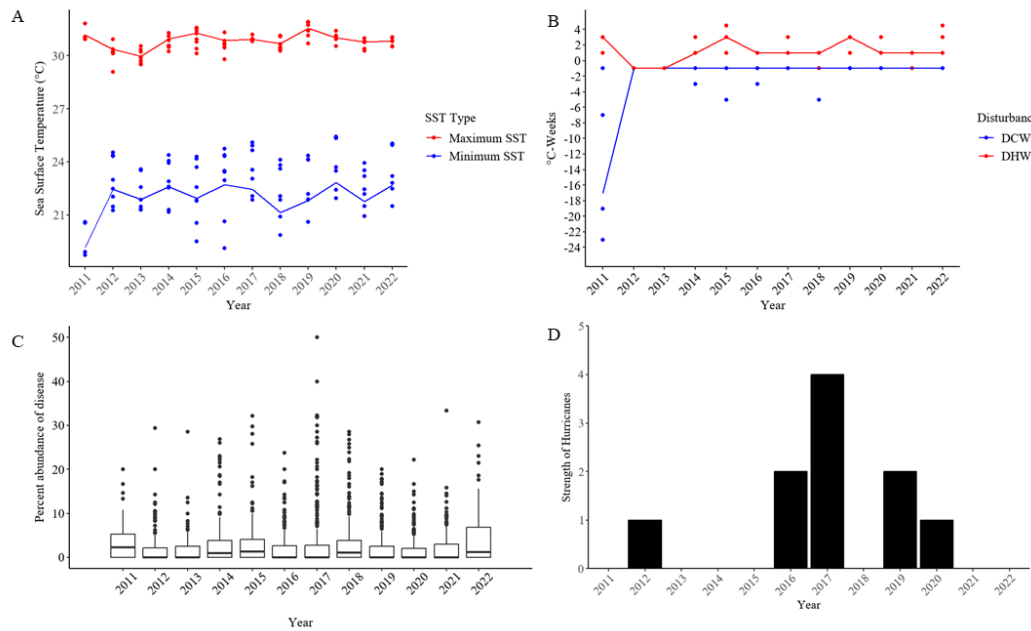


Figure 4: Temporal variation in the disturbance variables: (A) minimum and maximum SST, (B) DCWs and DHWs, (C) disease prevalence, and (D) the average strength of hurricanes. Lines for A and B are color-coded and represent average data values, where red represents heat stress (maximum SST and DHWs) and blue represents cold stress (minimum SST and DCWs). Points in A, B, and C represent individual data values

3.1.1.3. Temporal effects of disturbance on coral traits

Trait diversity showed a significant decline in both functional richness ($p = < 2 \times 10^{-16}$; Table 1) and Rao's quadratic entropy ($p = < 2 \times 10^{-16}$; Table 1). Trait redundancy, however, showed the opposite pattern. The modelled temporal effects on trait redundancy showed a significant shallow incline ($p = < 2 \times 10^{-16}$; Table 1). Additionally, average hurricane strength, percent abundance of disease, and minimum SST significantly impacted functional richness, Rao's quadratic entropy, and trait redundancy. However, DHWs and maximum SST only significantly impacted Rao's quadratic entropy and trait redundancy, and DCW had no significant impact (Table 1). The random effects of site also accounted for a significant portion of variation in functional richness, Rao's quadratic entropy, and trait redundancy (Table 1).

Table 1: GAMM model outputs for the models with the lowest AIC representing the temporal effects of disturbances on trait diversity (functional richness and Rao's quadratic entropy) and trait redundancy. The F-value/Chi squared value column represents f-values for functional richness models, as those used a gamma distribution, and represents chi-squared values for Rao's quadratic entropy and trait redundancy, as those used a beta distribution. Each individual table represents one model. Model A is the lowest AIC model of functional richness which uses minimum and maximum SST and not DHWs and DCWs. Model B is the lowest AIC model of functional richness which uses DHWs and DCWs and not minimum and maximum SST. Model C is the lowest AIC model of Rao's Quadratic Entropy which uses minimum and maximum SST and not DHWs and DCWs. Model D is the lowest AIC model of Rao's Quadratic Entropy which uses DHWs and DCWs and not minimum and maximum SST. Model E is the lowest AIC model of Rao's Quadratic Entropy which uses minimum and maximum SST and not DHWs and DCWs. Model F is the lowest AIC model of Rao's Quadratic Entropy which uses DHWs and DCWs and not minimum and maximum SST

A

Predictor	Random effect	Effective degrees of freedom	Reference degrees of freedom	Degrees of Freedom	F-value/Chi Squared	P-value
Minimum SST	No	-	-	1	6.418	0.011
Maximum SST	No	-	-	1	3.563	0.059
Average Strength of Hurricanes	No	-	-	1	20.558	5.8×10^{-6}
Percent abundance of disease	No	-	-	1	3.409	0.065
Year	No	3.397	3.764	-	251.100	$< 2 \times 10^{-16}$
Site:Year	Yes	55.914	56.000	-	708.300	$< 2 \times 10^{-16}$

B

Predictor	Random effect	Effective degrees of freedom	Reference degrees of freedom	Degrees of Freedom	F-value/Chi Squared	P-value
DCW	No	-	-	1	0.846	0.358
DHW	No	-	-	1	0.002	0.969
Average Strength of Hurricanes	No	-	-	1	0.569	0.451
Percent abundance of disease	No	-	-	1	0.090	0.765
Year	No	6.346	7.587	-	35.670	$< 2 \times 10^{-16}$
Site:Year	Yes	69.505	70.000	-	177.910	$< 2 \times 10^{-16}$

C

Predictor	Random effect	Effective degrees of freedom	Reference degrees of freedom	Degrees of Freedom	F-value/Chi Squared	P-value
Minimum SST	No	-	-	1	39.075	4.08×10^{-10}
Maximum SST	No	-	-	1	40.469	2.00×10^{-10}
Average Strength of Hurricanes	No	-	-	1	4.697	0.030
Percent abundance of disease	No	-	-	1	4.107	0.043
Year	No	3.457	3.803	-	94.840	$< 2 \times 10^{-16}$
Site:Year	Yes	68.600	70.000	-	9393.680	$< 2 \times 10^{-16}$

D

Predictor	Random effect	Effective degrees of freedom	Reference degrees of freedom	Degrees of Freedom	F-value/Chi Squared	P-value
DCW	No	-	-	1	0.096	0.756
DHW	No	-	-	1	18.595	1.62×10^{-5}
Average Strength of Hurricanes	No	-	-	1	1.969	0.161
Percent abundance of disease	No	-	-	1	1.859	0.173
Year	No	3.546	3.861	-	81.640	$< 2 \times 10^{-16}$
Site: Year	Yes	68.617	70.000	-	9285.640	$< 2 \times 10^{-16}$

E

Predictor	Random effect	Effective degrees of freedom	Reference degrees of freedom	Degrees of Freedom	F-value/Chi Squared	P-value
Minimum SST	No	-	-	1	44.639	2.37×10^{-11}
Maximum SST	No	-	-	1	18.228	1.96×10^{-5}
Average Strength of Hurricanes	No	-	-	1	4.643	0.031
Percent abundance of disease	No	-	-	1	3.976	0.046
Year	No	6.782	7.969	-	92.520	$< 2 \times 10^{-16}$
Site: Year	Yes	68.656	70.000	-	9932.200	$< 2 \times 10^{-16}$

F

Predictor	Random effect	Effective degrees of freedom	Reference degrees of freedom	Degrees of Freedom	F-value/Chi Squared	P-value
DCW	No	-	-	1	0.760	0.383
DHW	No	-	-	1	77.949	$< 2 \times 10^{-16}$
Average Strength of Hurricanes	No	-	-	1	12.744	3.57×10^{-4}
Percent abundance of disease	No	-	-	1	2.999	0.083
Year	No	3.860	3.986	-	284.300	$< 2 \times 10^{-16}$
Site: Year	Yes	55.837	56.000	-	37458.100	$< 2 \times 10^{-16}$

Disturbances significantly influenced temporal variation in trait composition (Table 2). DCWs and minimum SST significantly affected trait composition (Table 2). Interestingly, only DHWs and not maximum SST significantly affected trait composition (Table 2). However, disease prevalence, as well as the number and average strength of hurricanes did not significantly affect trait composition (Table 2).

Table 2: Linear regression results for the temporal effects of heat stress, cold stress, the number of hurricanes, the average strength of hurricanes, and the percent abundance of disease on trait composition. Results are broken down into two models, one with DHWs and DCWs, and one with minimum SST and maximum SST. Table A is the model with DHWs and DCWs and does not include minimum and maximum SST. Table B is the model with minimum and maximum SST and not DHWs and DCWs.

A

Predictor	Degrees of Freedom	F value	R ²	p-value
DCW	1	32.244	0.002	0.001
DHW	1	18.853	0.001	0.027
Number of hurricanes	1	2.477	>0.001	0.604
Average strength of hurricanes	1	1.467	>0.001	0.139
Percent abundance of disease	1	37.577	0.003	0.882
Year	1	69.377	0.005	0.001

B

Predictor	Degrees of Freedom	F value	R ²	p-value
Minimum SST	1	95.735	0.006	0.001

Maximum SST	1	104.613	0.007	0.058
Number of hurricanes	1	20.191	0.001	0.645
Average strength	1	10.002	>0.001	0.604
Percent abundance of disease	1	38.591	0.002	0.928
Year	1	37.182	0.002	0.941

3.1.1.4. Coral traits which connect to disturbance or temporal variation

Maximum corallite width explained the most about coral species responses to disturbance (Figure 6a). Twenty-two percent of species had maximum corallite widths greater than or equal to 14 mm (Figure 6a). Seventy-eight percent of species had maximum corallite widths less than 14 mm (Figure 6a). Within that 78% of species, the trait that most explained coral species response to disturbance was growth rate (Figure 6a). Twenty-four percent of species had a growth rate of greater than or equal to 13 mm-yr⁻¹ (Figure 6a). The remaining 54% of species had a growth rate of less than 13 mm-yr⁻¹ (Figure 6a). Within that 54% of species, the trait that explained coral species response to disturbances the most was also growth rate, where 30% of species had a growth rate of less than 4.9 mm-yr⁻¹ and 24% of species had a growth rate of greater than or equal to 4.9 mm-yr⁻¹ (Figure 6a). Each split in the regression tree represents a different response to disturbance, where the further to the left on the figure, the stronger the species ability to withstand disturbance.

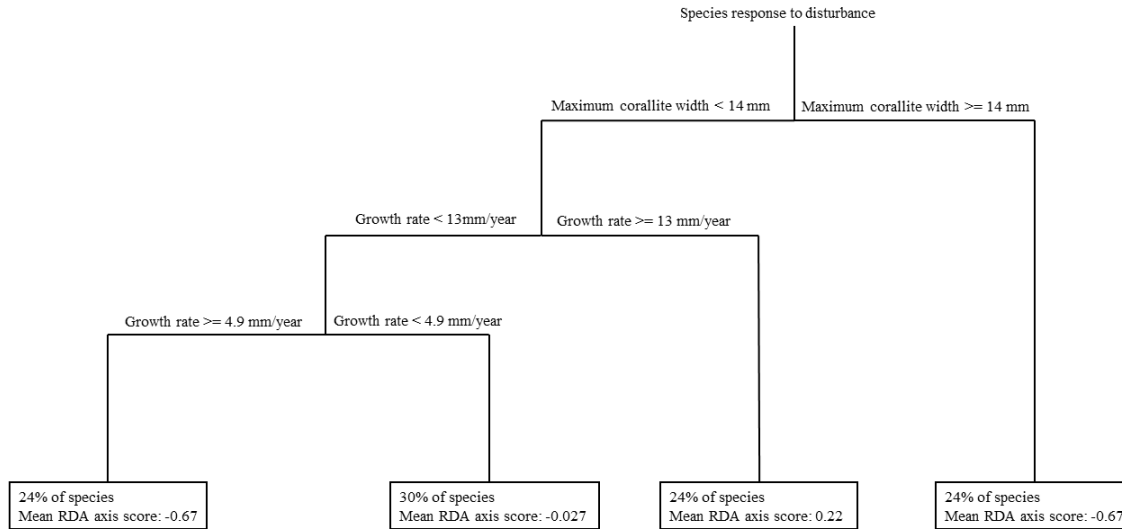


Figure 6: Influence of traits on species response to disturbance. This figure is a Regression tree analysis of the influence of species traits on species response to disturbance. Decision nodes represent specific trait values which influence species response to disturbance, and end nodes represent the percent of species with the combination of traits displayed by the decision nodes.

3.2. Objective II

3.2.1. Variation in trait composition between regions, sites, and species

The species cluster dendrogram revealed three major clusters of similarity in trait composition between the four dominant species observed in our surveys (Figure 7A). The three clusters were: (1) *Montastrea cavernosa*, (2) *Stephanocoenia intersepta*, and (3) *Porites astreoides* and *Siderastrea siderea*. The site cluster dendrogram revealed two major clusters of similarity in trait composition between the six sites (Figure 7B). The two clusters were: (1) Dania Beach, Hollywood, and North Bay Village, and (2) Fort Lauderdale, Key Biscayne, and Pompano. The habitat cluster dendrogram revealed two major clusters of similarity in trait composition between the four regions (Figure 7C). The two clusters were: (1) middle and outer reefs, and (2) inner and nearshore reefs.

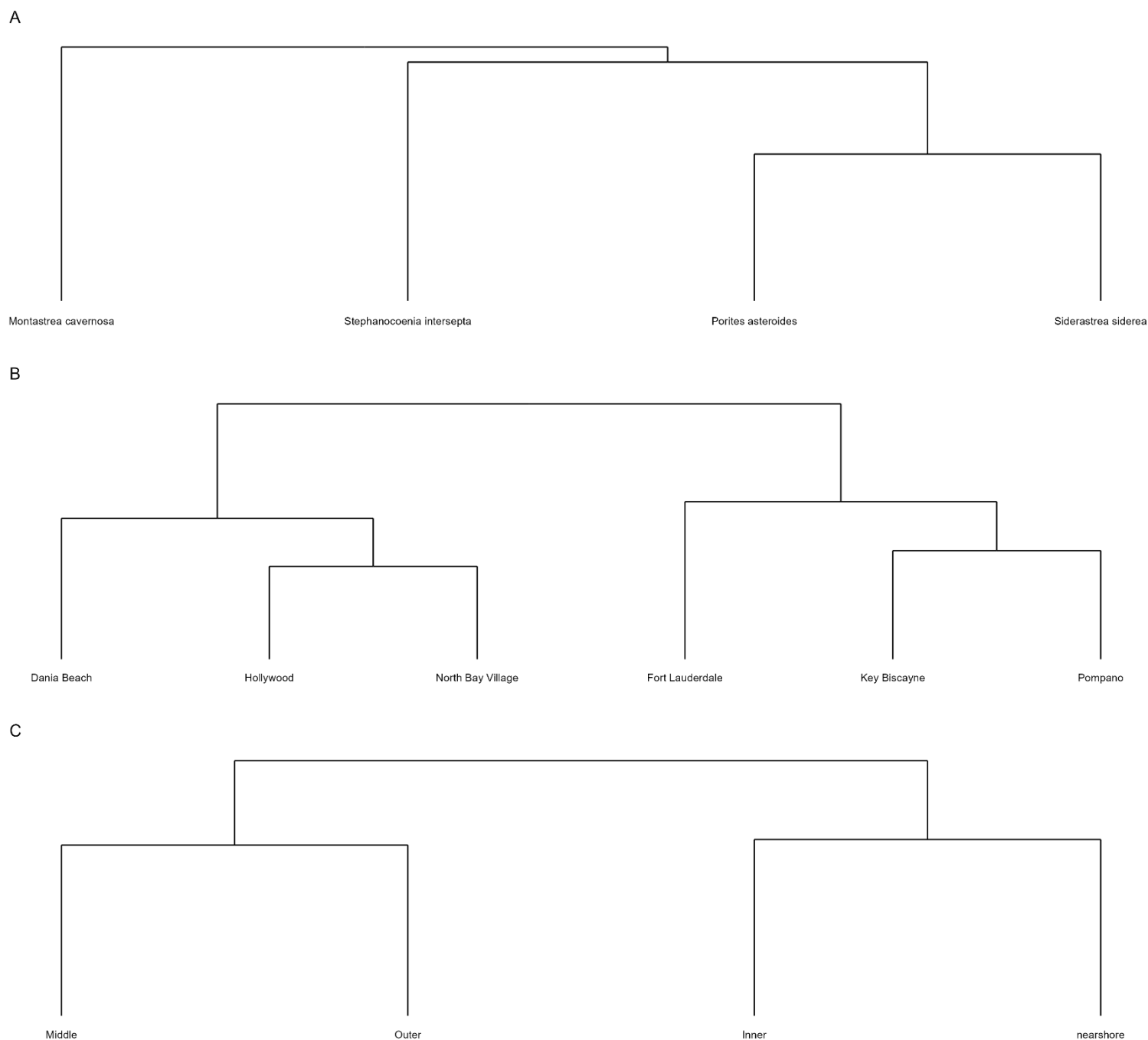


Figure 7: Cluster dendrogram displaying similarity in trait composition between (A) the four dominant coral species observed in our surveys of Florida's Coral Reef, (B) the six sites surveyed, and (C) the four habitats. The y-axis represents similarity where the

higher the split on the y-axis for each plot, the less similar the individuals are. Each cluster dendrogram was built from the in-situ data for the four dominant species.

The principal coordinates analysis of trait composition between species (Figure 8A) showed *Stephanocoenia intersepta* as the most dissimilar from remaining three species, most driven by growth form, especially submassive, and tissue thickness. The principal coordinates analysis of trait composition between sites (Figure 8B) showed Fort Lauderdale and Key Biscayne as the most dissimilar sites, most driven by corallite width, tissue thickness, volume compactness, and growth form. The principal coordinates analysis of trait composition between habitats showed all four habitats (nearshore, inner, middle, outer) to be equally similar in trait composition (Figure 8C). Similarity between habitats is most driven by corallite width, tissue thickness, volume compactness, and growth form.

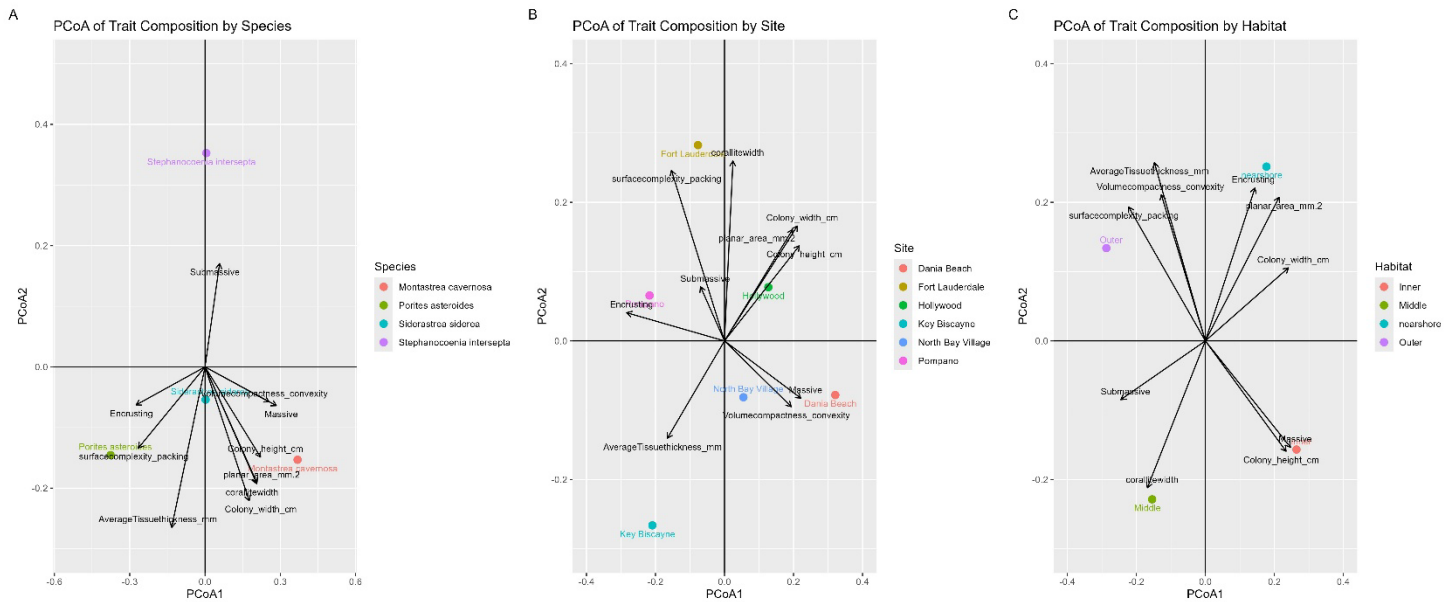


Figure 8: Principal coordinates analysis displaying a multidimensional representation of similarity in trait composition between: (A) species, (B) sites, and (C) habitat.

3.3. In-situ trait diversity and redundancy

None of the trait diversity or redundancy metrics significantly differed by site ($p = 0.2466$ for all metrics) or habitat ($p = 0.418$ for all metrics). While there was no significance, Key Biscayne had a slightly higher functional redundancy than the other sites (Figure 9).

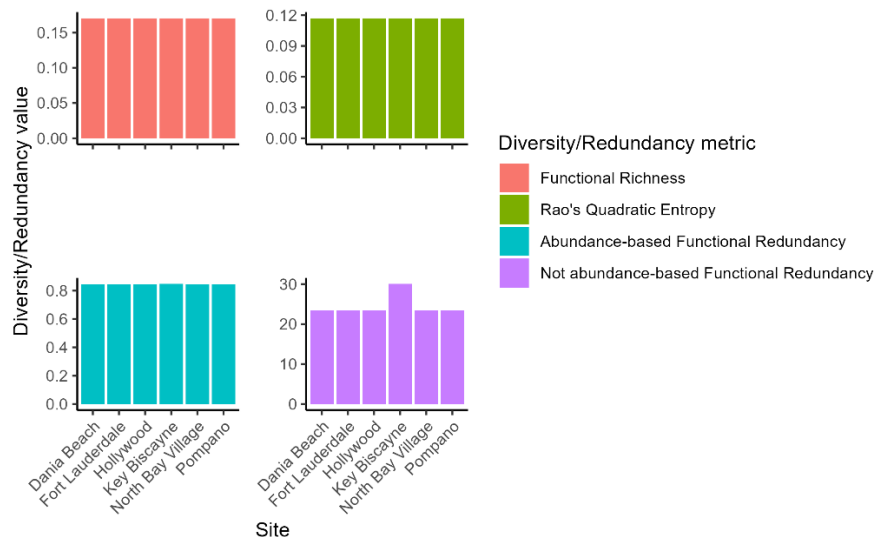


Figure 9: Variation in functional richness, Rao's quadratic entropy, functional redundancy weighted by abundance, and functional redundancy not weighted by abundance between sites on Florida's Coral Reef.

3.4. Ranking of coral species for restoration based on the presence of resilience traits and their contribution to increasing trait diversity and decreasing trait redundancy

Species were assigned an overall score based on individual scores of the presence of resilience traits (figure 6) and their contribution to increasing trait diversity and decreasing trait redundancy. Coral species varied in their overall score, in their score for resilience, and their score for their contribution to increasing trait diversity and decreasing trait redundancy. The *Orbicella annularis* complex, *Isophyllia sinuosa*, *Favia fragum*, and *Colpophyllia natans* had the highest overall scores (Figure 10), while *Helioseris cucullata*, *Mussa angulosa*, the *Mycetophyllia lamarckiana* complex, and *Phyllangia americana* complex had the lowest overall scores (Figure 10).

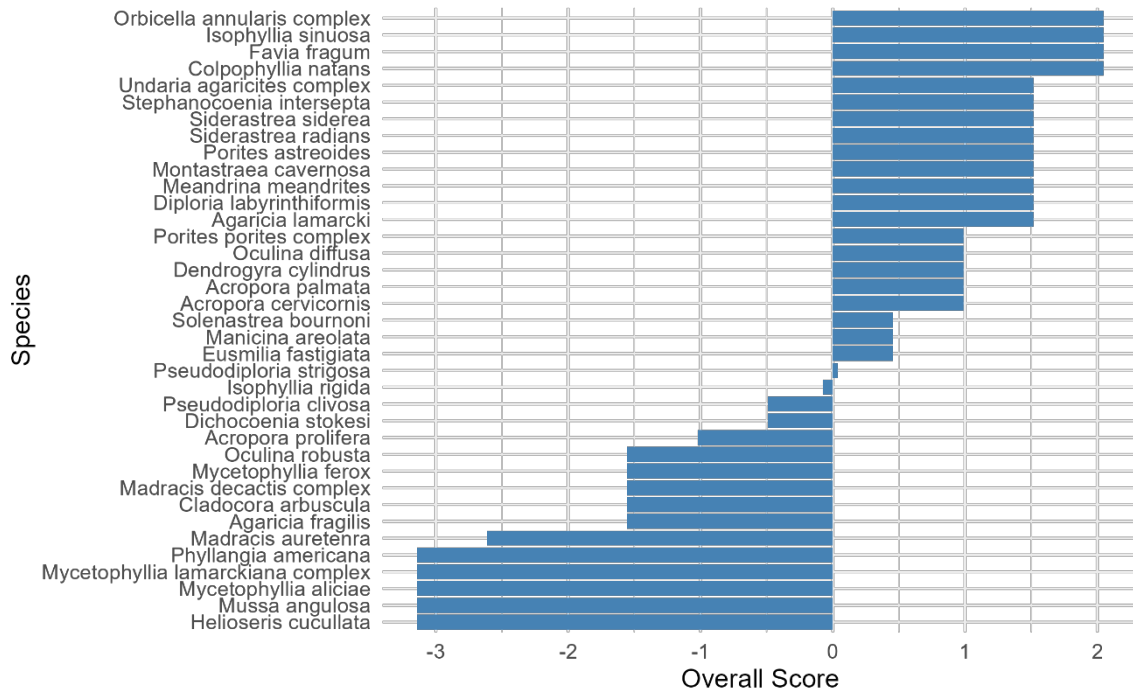


Figure 10: Ranking of coral species for restoration efforts based on individual scores of the presence of resilience traits and their contribution to increasing trait diversity and decreasing trait redundancy

4. DISCUSSION AND MANAGEMENT RECOMMENDATIONS

Florida's Coral Reef (FCR) had low trait diversity and high trait redundancy as well as largely unoccupied trait space. Recurrent disturbances drove declines in trait diversity, increases in trait redundancy, and shifts in trait space, suggesting that recurrent disturbances have resulted in a homogenization of traits in coral communities on FCR. Furthermore, Key Biscayne had the same level of diversity and higher redundancy compared to the other sites, suggesting that this site in particular has homogenized more than other sites. These findings suggest enhancing trait diversity through management and restoration is crucial, as trait diversity is low on FCR but essential for maintaining ecosystem functions, such as structural complexity and calcium carbonate accretion. This study offers a ranking system which scores coral species based on their resilience and ability to expand trait diversity. This ranking system could be used by restoration practitioners to include supporting trait diversity, and by extension ecosystem functions, in their efforts. Additionally, expanding monitoring efforts to include trait measurements would further support data-driven management and adaptive restoration planning.

In situ trait data revealed higher diversity and lower redundancy compared to trait values from global databases, suggesting that local measurements capture additional

variation important for understanding reef function. Incorporating *in situ* trait monitoring into existing programs can expand efforts to support coral resilience and ecosystem function. Future research should assess whether similar trait patterns are observed in other regions of FCR and explore the contributions of additional benthic taxa (e.g., octocorals, sponges) to overall trait diversity and trait space. Quantifying how the resilience traits identified in this study influence individual coral colony survival in response to specific disturbances, such as thermal anomalies and disease outbreaks, would be valuable to expanding resilience on FCR.

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