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HABITAT SUITABILITY MODELING LONG-TERM GROWTH AND HEALTHY COVER TRENDS OF STAGHORN CORAL (ACROPORA CERVICORNIS) OUTPLANTS IN THE LOWER FLORIDA KEYS

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Table of Contents

LIST OF TABLES

LIST OF FIGURES

opposed to the Surface Parameter tool. The Surface Parameter tool fits a surface to cells to calculate values, instead of previous tools which fit a plane to cells.

Figure D1: The Aspect tool, which fits a plane to a cell, and the Surface Parameter tool, which fits a surface to a cell, results in similar values of Northerness and Easterness.

Figure E1: Model results for percent healthy cover, using terrain attributes which fit a plane to a cell vs. a surface to a cell for slope, curvature, Northerness, and Easterness result in different model results with covariate significance. When fitting a plane to a cell, curvature is significantly correlated with healthy coral cover for corals older than two years old.

Figure F1: Model results for total and healthy growth, using terrain attributes which fit a plane to a cell vs. a surface to a cell for slope, curvature, Northerness, and Easterness result in different model results with covariate significance. When fitting a plane to a cell, distance from coast, terrain roughness, and HWE for total growth are no longer significantly correlated.

ABSTRACT

In the Florida Keys *Acropora cervicornis* has been targeted for restoration due to its importance as a reef building stony coral. Habitat suitability models have been utilized within restoration ecology to identify potential locations for outplanting. To date, habitat suitability models have used coarse spatial data of large areas throughout the Florida Keys, resulting in recommended outplant sites that restoration groups have financial and logistical limitations to access and regularly monitor, due to being far away. Additionally, outplanting success can vary widely within a limited space, necessitating improved predictive abilities of coral outplant success within a restoration site. With the advent of Structure from Motion, fine–scale, site specific, digital elevation models can be created to support habitat suitability model development. In this study, generalized linear mixed models use extracted seafloor terrain attributes and environmental variables to identify within site locations of high *A. cervicornis* growth and healthy coral cover of long-term outplants. Percent healthy coral cover significantly decreased after two years of outplantation, with a submodel of just corals less than two years old unable to identify environmental conditions associated with higher percent healthy cover. Depth, distance from coast, less rough terrain, and proximity to the spur-and-groove interface, are correlated with higher percent healthy coral cover. Convex terrain, rough terrain, marine heat, and cold waves are correlated with decreased coral growth. Increased slope, distance from coast, and high wind events are correlated with higher coral growth. Cumulatively, these results emphasize the importance of long-term monitoring and fine-scale surveying when making coral outplant site recommendations.

Chapter 1: Introduction

1.1 Coral Decline

In the past half century, corals around the world have been decimated by mounting climate change induced high intensity thermal and wind events (IPCC, 2018). Coupled with increasing threats of disease, anthropogenic run off, and overfishing much of the coastal reefs around the world are expected to be gone in the coming decades (Golbuu et al., 2011; Valentine & Heck, 2005; Williams & Miller, 2005; IPCC, 2018). Dominating stony coral reefs in the Caribbean and Florida Keys have shown to be especially vulnerable (Precht et al., 2016) and have suffered from climate change induced stressors, shifting in composition and range (Toth et al., 2019). One such stony coral, *Acropora cervicornis*, has been severely affected, decreasing in abundance by an estimated 95% since the 1970s and thus labeled critically endangered on the IUCN Red List (Crabbe et al., 2022). As the coral species declines, much of the Florida Reef Tract will lose essential reef structure (Acropora Biological Review Team, 2005). The acroporid species initially declined due to white band disease (Aronson & Precht, 2001), but in combination with other diseases and increasing ocean temperatures, the coral has not been able to recover.

Several diseases threaten *A. cervicornis*, including black band disease (BBD), white band disease (WBD), and Caribbean ciliate infection (CCI). Infection can be difficult to tell apart (Bruckner, 2002; Verde et al., 2016), making management and restoration difficult. Black band disease is caused by cyanobacteria and is identified by the black band separating the healthy tissue from the encroaching dead tissue. No organism has been found to singularly function as a vector for spreading BBD, due to the complex microbial community not carried within a singular organism needed to establish infection. Instead, BBD is spread through multiple corallivorous invertebrates causing lesions on the tissue for microbes within the water to colonize (Nicolet et al., 2018). Less is known about the cause of white band disease, but there is evidence to support it being a bacterial infection (Kline & Vollmer, 2011). CCI is an opportunistic infection, colonizing within damaged and lesioned coral tissue caused by corallivorous invertebrates or corals already infected by BBD or WBD (Verde et al., 2016). *A. cervicornis* is especially vulnerable to CCI, suffering higher rates of mortality than other reef building corals (Verde et al., 2016). Lesions for disease to enter through can also be caused by high thermal and wind stress events (Rodriguez, 2008).

While *A. cervicornis* can recover, to a limited degree, from marine heat wave (MHW) events (Baird & Marshall, 2002) and some genets exhibit a higher tolerance to elevated temperatures (Foo & Asner, 2020; Genevier et al., 2019), episodic high stress events have been shown to have a higher impact on coral recovery when they occur more frequently (Goreau & Hayes, 2021). Consequently, with increased MHW intensity and duration, *A. cervicornis* recovery will likely decrease. Marine cold wave (MCW) events will decrease in the coming decades as climate change continues and have resulted in fewer studies reporting on their effect on coral health (IPCC, 2018). Despite this, MCWs continue to threaten coral restoration as exemplified by the cold-water event in southern Florida in 1976-1977 (Porter et al., 1981) and 2010 (Colella et al., 2012; Lirman et al., 2011). This event caused severe mortality in patch reef environments that had previously shown resistance to disease and marine heat wave events. This was particularly true for *A. cervicornis*, which has shown survivability and growth to be especially negatively affected due to its thermal sensitivities compared to other corals (Kemp et al., 2016; van Woesik et al., 2020). Unlike marine heat and cold wave effects on corals, those of high wind events (HWE) are less known. While some studies have shown that high wind events, such as tropical cyclones and hurricanes, have the capacity to induce mortality in corals and decrease coral growth (Goergen et al., 2019; Muko et al., 2013; Riegl et al., 2009), others show hurricane induced cooling mitigates bleaching (Carrigan & Puotinen, 2014; Manzello et al., 2007) and increases coral fragmentation, promoting reef growth through asexual propagation (Omori, 2019). These threats have resulted in increased efforts towards promoting resilient reefs, capable of withstanding and recovering from disturbance.

1.2 Coral Restoration

Reef restorative research is flourishing to combat mounting disease and climate change induced stressors driving coral decline worldwide (Hughes et al., 2017). Coral transplantation, the propagation of asexually reproduced coral fragments, started in the 1970s (Maragos, J., 1974). By the early 2000s, in response to declining coral populations, nursery grown corals were reared in labs and outplanted in the marine environment (Herlan, J., & Lirman, D., 2008; Lirman, D., et al., 2010) *A. cervicornis* has been one of the primary targeted species for restoration due to its importance as a reef builder, for growing quickly, and being long-lived (Devlin-Durante et al., 2016; Hughes, 1985; Irwin et al., 2017). Methodologies for transplantation/outplantation and initial success rates of *A. cervicornis* have since been explored and include sexual and asexual propagation, methods for fixing the corals to the marine environment, threats of corallivores (coral eating species), and growth and survivorship (O'Donnell et al., 2017; Omori, 2019). Long-term monitoring of coral outplants is often not realized, nor influential in informing outplanting techniques, and thus sustained recovery is not clearly established (Fox et al., 2019; Boström-Einarsson et al., 2020). Consequently, there is a knowledge gap in monitoring the success of coral outplants over multiple years. Of the few long-term studies that have occurred, research suggests that initial coral survivability and growth is high, however both decrease after two years (Ware et al., 2020).

To better understand optimal locations for corals to occupy, habitat suitability models have been developed to support restoration efforts. Habitat suitability models (HSMs) and ecological niche models use environmental and physical characteristics to identify suitable habitat for species of interest. These models help to improve the understanding of ecological systems (Hirzel & Le Lay, 2008), identify important influences in suitable habitat for organisms (van Woesik et al., 2020), support spatial planning (Rengstorf et al., 2013), identify vulnerable locations for invasive species to invade and occupy (Goldsmit et al., 2018), and understand species range expansion due to climate change (Couce et al., 2013). The potential for HSMs to predict favorable niches for endangered coral species has been applied widely. This includes models of wild coral population occurrence (van Woesik et al., 2021), coral recruitment (Riegl et al., 2009), and global coral responses to warming and ocean acidification (Couce et al., 2013). These models provide insight into the resilience of wild coral populations and make predictions for how coral populations will change according to climate projections. Given the increased interest in coral restoration, HSMs have the potential to identify optimal sites for *A. cervicornis* outplantation. Variables utilized previously in projecting *A. cervicornis* presence or improved survivability include sea surface temperature, turbidity, and water flow. Higher temperatures and larger temperature ranges were not favorable for *A. cervicornis*, while moderate turbidity helped to mitigate temperature fluctuations and UV radiation (van Woesik et al., 2020). Higher water flow delivered food (dissolved organic matter), thereby increasing mass transfer and growth (Banister & van Woesik, 2021; van Woesik et al., 2020). HSMs of multiple Florida Reef Tract corals demonstrate higher wave energy and distance from coast provided suitable habitats for other corals. Bathymetric characteristics have also routinely been utilized in HSMs due to their capacity to consistently predict where corals in the Florida Keys are likely to be found (Tong, 2013a; Tong et al., 2013b; Van Woesik et al., 2020) due to bathymetric influence on flow regimes (Dolan et al., 2008; Guinan et al., 2009; Howell et al., 2011). From these environmental conditions, HSMs show *A. cervicornis* has limited suitable habitats within the Florida Key Reef Tract, constrained to the fore and back reef of the lower and upper Florida Keys, the Dry Tortugas, and nearshore Broward-Miami reefs (Ware et al., 2020; van Woesik et al., 2021).

Current monitoring efforts and habitat suitability models, however, are inadequate towards supporting outplanting efforts. Current models often use wild populations of high *A. cervicornis* occurrence and tend to look at large swaths of ocean area with coarsely resolved environmental data (van Woesik et al., 2020). Environmental characteristics are often collected through remote sensing efforts, such as satellites with 0.25 to 1km resolution. Coarsely resolved environmental data results in many recommended sites from HSMs that are financially and logistically difficult to access for outplantation and recurring monitoring (E. Bartel, Personal Communication,12/7/2021). Predicted suitable habitat can be hundreds of square kilometers, while many restoration activities occur at finer spatial scales of meters long outplant sites. Interestingly, within these finer spatial scales, coral survival throughout the same outplant site is highly variable (Ware et al., 2020), suggesting a deeper understanding of the environment and coral success is needed. Additionally, coral outplant's growth and survivorship perform differently than wild and transplanted coral populations (Lirman et al., 2010; Omori, 2019), making these models imprecise in recommendations for outplants. To develop HSMs helpful to restoration groups, fine-scale HSM of long-term outplanted corals must be tailored to restoration group capabilities to inform outplantation.

1.3 Aims of the Thesis

The purpose of this study is to create fine-scale habitat suitability models to determine minute differences of seafloor terrain within a site that contribute to outplants growth and percent healthy cover. Fine-scale bathymetric and environmental data can be curated for such HSMs using Structure-from-Motion (SfM) photogrammetry, unique in its capacity to develop three-dimensional terrain models which provide insight in terrain structure and complexity (Burns et al., 2015; Fukunaga et al., 2019; McDowall & Lynch, 2017). The high-resolution DEM is unique to HSMs utilization, due to being several orders of magnitude finer scale than many other HSMs that have spatial resolutions of 0.25km to 1 km. This fine-scale bathymetric data can inform water flow regimes and subsequent delivery of food to corals, mitigation of temperature fluctuations, corallivore presence, and disease (Barott & Rohwer, 2012; Borland et al., 2021; Chong-Seng et al., 2011). This information in turn helps define ecosystem health and distribution/abundance of biota (Pygas et al., 2020). Additionally, the detailed nature of terrain models, developed from *in-situ* stereo-imagery, provides insight of biotic morphological influence on flow regimes and individual coral health, unavailable from satellite and sonar derived bathymetry (Burns et al., 2015; Burns et al., 2019; Combs, I. R., 2019; Fukunaga et al., 2019).

This study evaluates *A. cervicornis* growth and healthy cover trends following outplantation, associating terrain attributes and environmental characteristics with successful corals in both the short-term and long-term, and the influence episodic high-stress environmental events have on coral outplants throughout their lifetime. Total and healthy growth – the change in total skeletal size and healthy tissue size since outplantation per year of outplantation – will give an indication where in the fine-scale there is optimal mass transfer and minimal stress

(Fabricius, 2011; Manzello, 2010). Percent healthy cover – the percent of a coral outplant with healthy tissue cover – will give an indication of where corals are least exposed to disease, are more resilient to disease, or where corals are best able to recover from infection (Shore & Caldwell, 2019). Distance from coast, distance from the spur and groove interface (hereafter reef edge), distance from other *A. cervicornis*, time outplanted, and SfM derived bathymetric terrain attributes (depth, slope, curvature, aspect, and roughness) for each coral were included as predictor variables in the HSMs. Annual average intensity of high wind events, marine heat waves, and marine cold waves per duration of event were included to assess high stress events' influence on growth and percentage of healthy coral cover.

Chapter 2: Methods and Materials

2.1 Outplanting

Percent cover and growth of *A. cervicornis* were determined at eight sites in the lower Florida Keys. Corals were outplanted by Mote marine laboratory (Table 1). Fragments outplanted ranged from 250 to 1000 fragments per outplant site and corals initial sizes ranged from 3cm to 50cm at their longest length. Except for the 3cm corals plugs at ADAC1, all other sites had clusters of five coral fragments outplanted together which would merge with each other over time. Corals were affixed to the seafloor using either nails and cable ties; nails, cable ties, and epoxy; or affixed to plugs with epoxy. A variety of genotypes were utilized within each outplant group to promote genetic diversity and resilience. Corals were outplanted to Sand Key, Eastern Dry Rock, M32, ICC1, and ADAC1 (Table 1, Fig. 1). All sites reside within the Florida Keys National Marine Sanctuary (FKNMS). FKNMS disallows any harming or removing of corals, dumping waste, or dredging (National Marine Sanctuary, 2015b). Additionally, Eastern Dry Rock and Sand Key are sanctuary preservation areas (SPA) in which removal or harm to marine life within the preservation area is prohibited. However, catch and release fishing by line trolling is allowed in Sand Key (National Marine Sanctuary, 2015a).

Table 1: Coral outplant group and date outplanted

Outplant Group	Outplant Date
T3	7/8/2017
S4	9/11/2018
S6	3/25/2019
M32-2	8/9/2019
M32-3	5/6/2020
ICC1	12/10/2020
ADAC1	10/5/2021
T16	2/11/2022

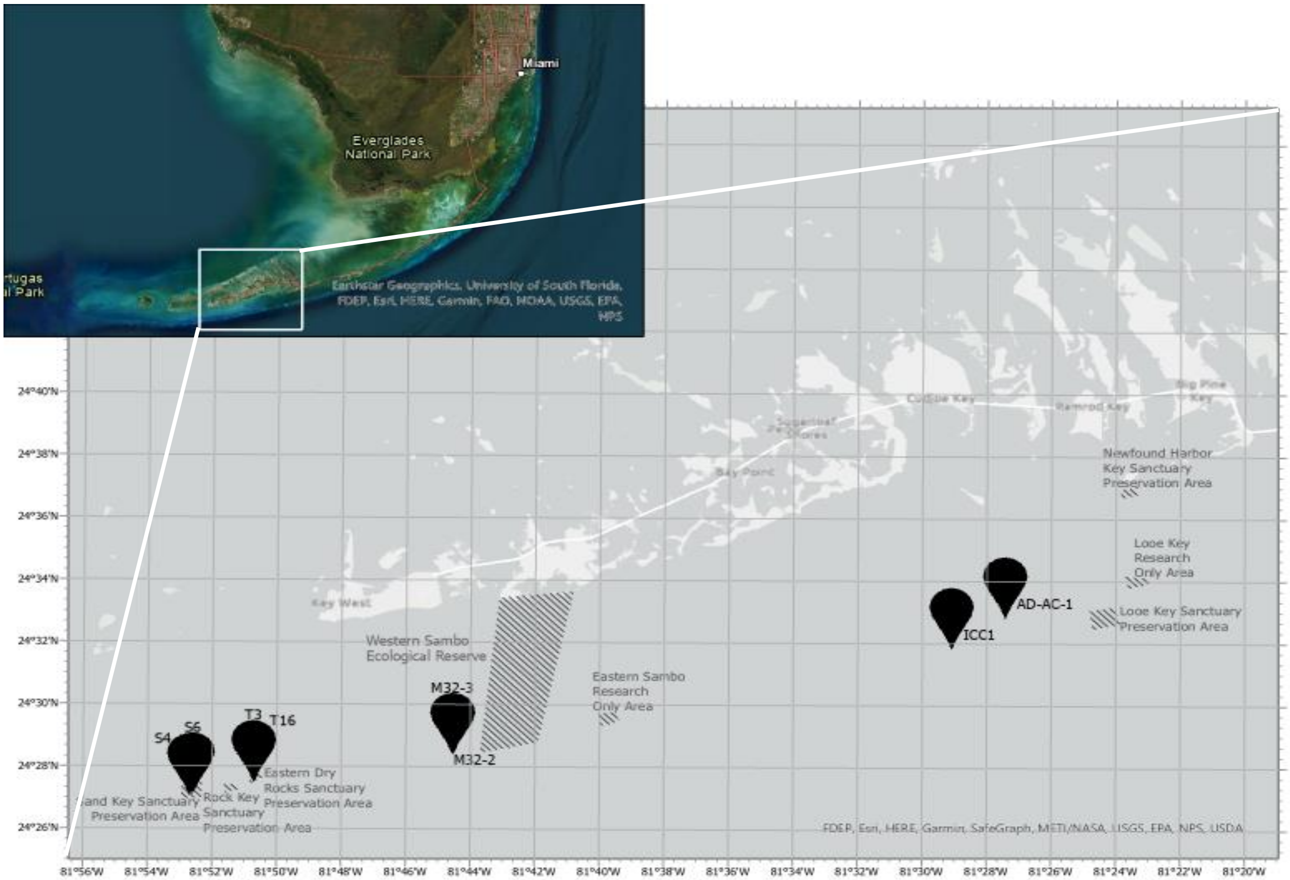

Figure 1: Eight survey sites within the lower Florida Keys to west of Key West (S4, S6, T3, T16, M32-2, M32-3, ICC1, and ADAC1). Shaded areas refer to sanctuary preservation areas and research only areas.

2.2 Image Collection

Eight coral outplant locations were surveyed in June of 2022, and one of the eight (ICC1) was previously surveyed the year before in July of 2021, resulting in nine outplant surveys. Two surveys occurred in Sand Key, two in Eastern Dry Rocks, two in M32, one in ICC1, and one at ADAC1. Coral outplant ages ranged from 129 to 1,788 days. All sites, except ADAC1, are on the forereef of the Florida Reef Tract and are composed of spur and groove geomorphology. Spur and groove are coral reef ridges (spurs) separated by sandy channels (grooves) (Eugene

Shinn, 1963). ADAC1 is a patch reef, an isolated reef outcropping separated by other reefs by sandy surrounding halos. Images were collected in 10X30m plots at all sites, except ADAC1 that had a 10X60m plot. Coded targets, which additionally functioned as scale bars, were systematically placed throughout each site in a grid formation. Images were taken with two Canon A70D DSLR cameras with a 20mm lens housed within an Aquatica A20D. Planar images of the seafloor were collected in a lawn-mower survey pattern, to facilitate co-register images and limit distortion. Cameras simultaneously took photos, resulting in over 80% image overlap. Depth measurements taken from a dive computer accounted for the four corners of each 10X30m or 10X60m site.

2.3 Three-dimension Terrain Model

Orthomosaics, 3D terrain models, and digital elevation models were constructed from Agisoft Metashape Professional V1.2.6 software. Agisoft was used due to thus far yielding optimal photogrammetric products (Sona et al., 2014). High resolution model construction was developed as described by Burns et al. (2015). Permanent control points, galvanized nails hammered into the bed rock and epoxied at the base to the seafloor, were georeferenced using a GARMIN system on-board the vessel for image reconstruction. *A. cervicornis* cover was quantified from orthomosaics (described below) (Fig. 2). Cover measurements were ground-truthed with *in-situ* measurements.

a. b.

Figure 2: Isolated image of *A. cervicornis* from site ICC1 within the orthomosaic (a) and the same corals from a lateral view within the 3D terrain model and validated height measurement (b)

2.4 Coral Cover

Feature class polygons were created to overlay healthy coral cover and total coral cover. Healthy cover was identified by orange/beige tissue without any bacterial mat growth. Total coral cover was all skeletal tissue cover. Coral cover was then classified by fragment, wild (non-outplanted), and outplanted corals. Only one site, ADAC1, had wild coral populations within the survey plot and were easily identifiable, as they were geographically distant from the outplants and much larger than the recently outplanted 3mm coral plugs. Coral cover polygons were attributed with number of outplanted fragments within an aggregate: ADAC1 outplants were all singular plugs; other sites were composed of five fragment aggregates; older sites (S4, S6, T3) composed of five fragment aggregates fused together to form a mass of thickets. Average coral fragment cover at time of outplantation was utilized to account for variations between initial size in calculating growth. Percent healthy tissue cover is the percentage of total coral cover with healthy tissue. Total coral growth is the change in coral cover size since outplantation. Healthy growth is the healthy coral cover tissue size change since outplantation. Growth could be negative due to decreasing cover from fragmentation (total and healthy growth) and disease (healthy growth).

2.5 Covariates

2.5.1 Bathymetric and distance characteristics

Structure-from-Motion digital elevation models (DEM) with a resolution of 0.1mm to 8mm were imported into ArcGIS (ArcGIS Pro 3.0, Environmental Systems Resource Institute), presented in UTM 17 zone projection, datum WGS84. Digital elevation models were standardized, utilizing the resample tool in ArcGIS Pro, to 8mm and were georeferenced to align exactly over the orthomosaics to ensure accurate sampling terrain attributes around corals. To attribute seafloor terrain variables to coral cover, a 0.1m buffer around each coral polygon was created. Associating seafloor terrain attributes - calculated using the Spatial Analyst toolbox in ArcGIS Pro - with total coral skeletal cover were extracted using ArcGIS Pro ModelBuilder for each coral outplant and included as covariates in the HSM (Fig. 3).

From the DEM, the surface information tool extracted maximum depth residing within the buffered feature. Slope, profile curvature, and aspect were extracted using the Surface Parameter tool, due to the tools capacity to extract accurate terrain values within fine-scale resolution raster (Kopp, 2/21). Single cell values calculations were made from an eleven-by-eleven cell window (surrounding 40mm) to facilitate extracting terrain values perceivable by the human eye and can therefore be translated to recommendations for restoration groups. Slope measured benthic steepness in degrees, with 0^{o} as horizontally flat, and 90^{o} indicates vertical.

Curvature calculated the second derivative of slope, thereby identifying rapid changes in slope or aspect. The standard curvature calculation combines profile and planform curvature values, quantifying directional changes in slope or aspect within the cell windows, and increase with terrain complexity (Blaga, 2019; Burns et al., 2015). Within ArcGIS positive profile curvature values represent convexity and negative values represent concavity. Aspect is the direction (360^{o}) of the terrain face. For model analysis aspect was separated into "Northerness" (cosine of aspect) and "Easterness" (sine of aspect). A terrain roughness raster, which calculates surface elevation value unevenness (Day & Chenoweth, 2013), was constructed, in accordance with Evans (1972, eq. 1). The Focal Statistics tool within the spatial analyst toolbox, which computes a statistical value from a given cell window neighborhood, extracted mean, minimum, and maximum values from the DEM for each cell within a three-by-three cell window (surrounding 8mm).

$$Roughness = (FSmean - FSmin) / (FSmax - FSmin) \quad (1)$$

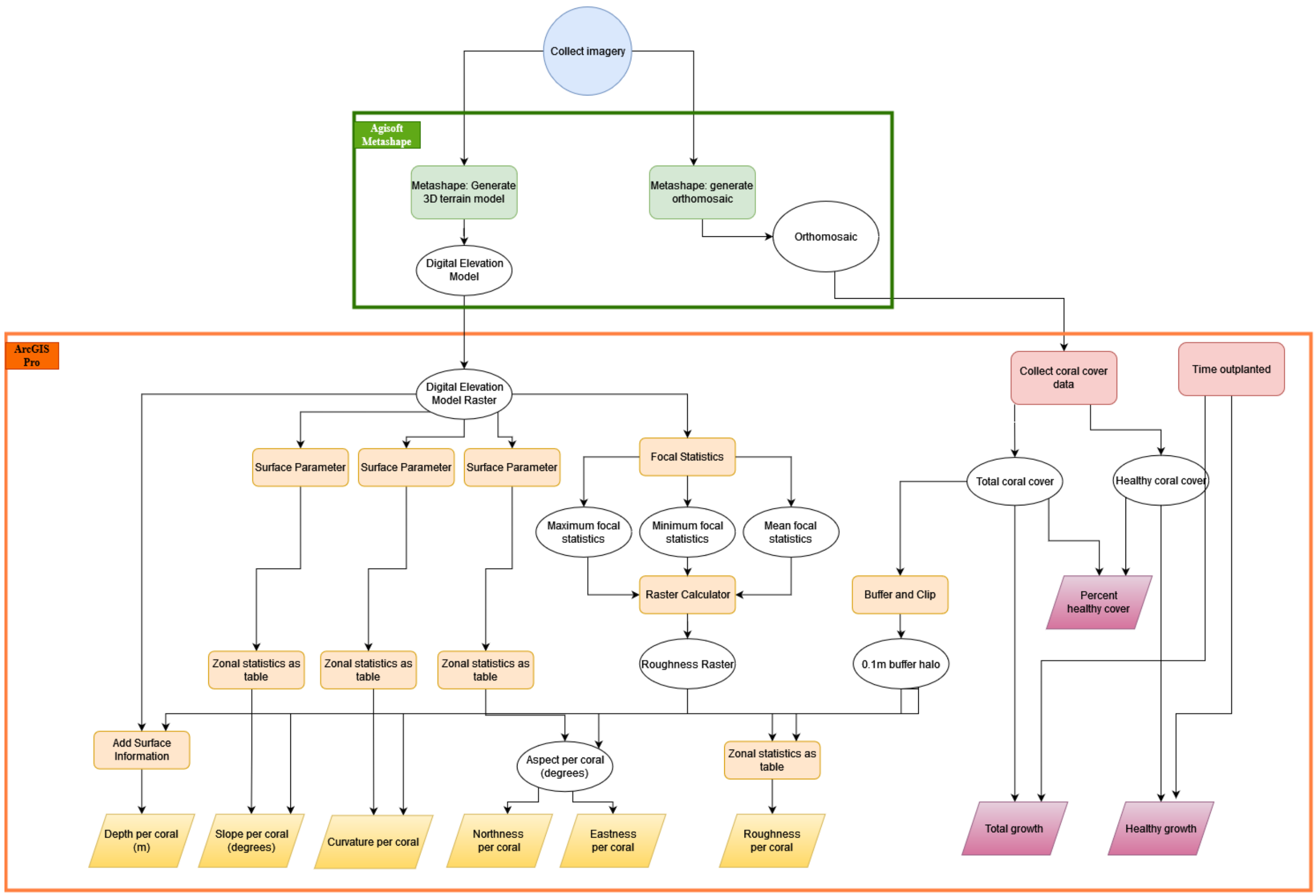

Figure 3: Methodology workflow from imagery collection in the field, DEM and orthomosaic construction in Agisoft Metashape, quantifying growth and healthy coral cover, and extraction of terrain attributes within ArcGIS Pro.

All coral outplant sites, apart from ADAC1, were in spur and groove reef terrain. The Euclidean distance of *A. cervicornis* from the spur/groove interface – indicated by a rapid drop in depth of at least 1m – and from the coastline was calculated for each coral using the spatial analysis patch tool in ArcGIS Pro.

2.5.2 High intensity events

Marine temperature and wind data were collected from Sand Key, Sombrero, and Key West NOAA buoys. Heat waves and cold waves followed Hobday et al. (2016), defined as five days or more of water temperatures exceeding the 90^{th} percentile (heat wave) or as five days or more of temperatures below the 10^{th} percentile (cold wave) of a 30-year historical base-line. This day-specific definition of marine heat wave and cold wave events accounts for thermally sensitive biological processes (such as reproduction), so that cold waves can occur in summer months and vice versa. Duration and intensity were defined by the number of days within a heat/cold wave event and the number of degrees exceeding or falling below the $90^{th}/10^{th}$ percentile, respectively. To avoid collinearity with time, annual average heat and cold wave intensity per duration of time throughout the coral's lifetime was used in the model. High wind events were any day(s) when the average daily wind speed exceeded 12.78 knots, the average sustained wind of a tropical storm (Goergen et al., 2019). High wind events were similarly transformed as MHW and MCW to avoid collinearity with time.

2.6 Statistical and Model Analysis

Coral fragments and wild corals were excluded from analysis. All statistical analysis and models were run in R (RStudio Team, 2020). Coral growth (total and healthy) deviating from zero was determined utilizing a t-test. Differences among sites in growth and percent healthy cover were evaluated using a one-way Analysis of Variance (ANOVA), with a null hypothesis of no differences among sites. If differences were observed a post-hoc Tukey's HSD ($p < 0.05$) was used to determine which sites were different.

A generalized linear mixed model (GLMM), operating within a frequentist statistical framework, was run using the glmmTMB package in R (Brooks et al., 2017a; Brooks et al., 2017b). Models were run of the entire sample of corals collected and submodels were run of subset populations if dramatically different trends in growth or percent healthy cover were observed. Model selection took the form of excluding highly correlating variables. No covariates were excluded in the models for growth and percent healthy cover due to adequate sample size, but submodels excluded highly correlating variables due to reduced sample size. Covariates, except time, were standardized to z-score values. The resulting model coefficients of the environmental covariate are the change in cm^2/yr for every change in standard deviation in the environmental covariate. The percent composition of a coral outplant with healthy tissue cover utilized a beta-distributed GLMM using a logit link function to doubly bound response values between 0% and 100%. Due to logit link limitations, healthy percent cover had to reside within values $0<y<1$ and could thereby not equal 0% healthy or 100% healthy. To address this, corals appearing 0% healthy or 100% healthy were transformed from values of 0 or 1 to 0.001 or 0.999, respectively. Transforming these values accounted for undetected diseased or healthy tissue cover by the surveyor for all corals. Separate models for corals in early stage and older stages of life were run to compare influences throughout an outplanted corals lifetime. Healthy and total cover utilized a Gaussian distribution. For all models, sites were run as random effects. Model diagnostics were visually inspected and affirmed from the "Performance" package and the Akion Information Criterion. Model convergence was affirmed from the glmmTMB hessian statistic.

Chapter 3: Results

After wild and fragmented corals were excluded 588 observed corals were included in the niche model. M32-3 had the most (105) and site T3 had the fewest (27) coral outplants collected within the orthomosaics. The deepest coral outplant locations were in T16 (8.35m) and shallowest were T3 (6.44m). The steepest coral outplant locations were in site M32-2 (37.73°)

and least steep were T3 (23.99°). The least rough coral outplant locations were in site SK6 (0.471) and ICC1 had the greatest roughness (0.493). The most concave coral outplant locations were in S6 (-2.148 rad/m) and the most convex locations in ADAC1 (3.119 rad/m). Covariates exhibited minimal collinearity except for distance from reef edge and high wind effects (R^2 = -0.80), which is completely coincidental. The model of young and old corals, utilizing data subset by coral outplant age, exhibited high collinearity of high intensity events with each other, with distance from the reef edge, and with depth.

3.1 Percent Healthy Cover Model

All coral ouplants, apart from those at ADAC1, showed some signs of disease. Site T3 within eastern dry rock and the oldest site within the study had the lowest mean percent of healthy coral cover. Percent of healthy cover decreased over time (GLMM, z = -2.634, p = 0.008). Healthy coral cover did not differ between T16, ADAC1, and ICC1 from 2021 and 2022, all of which are sites with corals less than 2 years old. Healthy coral cover did not differ significantly between M32-3, M32-2, S6, S4, and T3, all of which are sites with corals greater than 2 years old. Coral cover in sites with corals less than two years old differed significantly in healthy coral cover to sites with corals older than two years (ANOVA, $F_{8,579}$ = 30.89, p < 0.001). After two years of outplantation corals completely diseased, with no discernable healthy tissue coverage (0% healthy coral cover), and therefore assumed to be dead appeared. Percent healthy cover was variable across and within sites (Fig. 4). Of the 588 corals, 261 exhibited no disease and 41 exhibited no healthy cover. The site with the most corals with no healthy tissue was M32-2. Coral outplant sites within Sand Key exhibited higher percent healthy cover trends than other sites with older corals (Fig. 4).

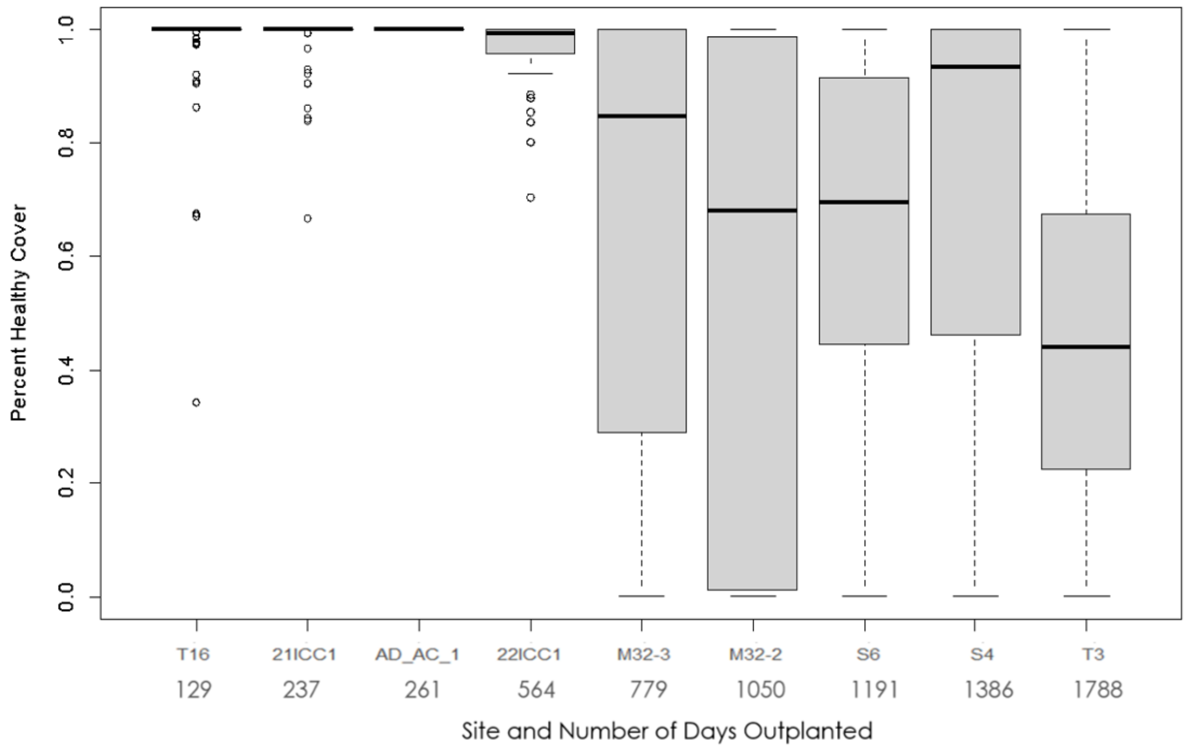

Figure 4: Percentage of healthy cover at each site in increasing time spent outplanted from left to right. Box plot shows the median, and upper and lower quartiles.

All following models converged according to the Hessian statistic and had AIC values of -1646.86 (all corals), -1118.504 (young corals), and -673.1902 (old corals). Model results of all corals show increasing distance from coast (GLMM, $z = 2.104$, $p = 0.035$), decreasing distance from the reef edge (GLMM, $z = -2.021$, $p = 0.043$), increasing depth (GLMM, $z = 2.579$, $p = 0.009$), and decreasing roughness (GLMM, $z = -6.280$, $p < 0.001$) correlated with higher healthy coral cover (Fig. 5a). Separate models for corals outplanted for less than two years ("young") and more than two years ("old") excluded high intensity events as covariates due to collinearity with each other and no evident effect on percent healthy cover for all corals. Subsequent models of young vs. old corals attribute the correlating relations come from older corals; no environmental variables could predict percent healthy cover in the first two years of outplantation. Increasing depth (GLMM, $z = 2.473$, $p = 0.013$) and decreasing roughness (GLMM, $z = -6.201$, $p < 0.001$) correlated with healthy coral cover in corals ≥ 2 yrs old (Fig. 5b).

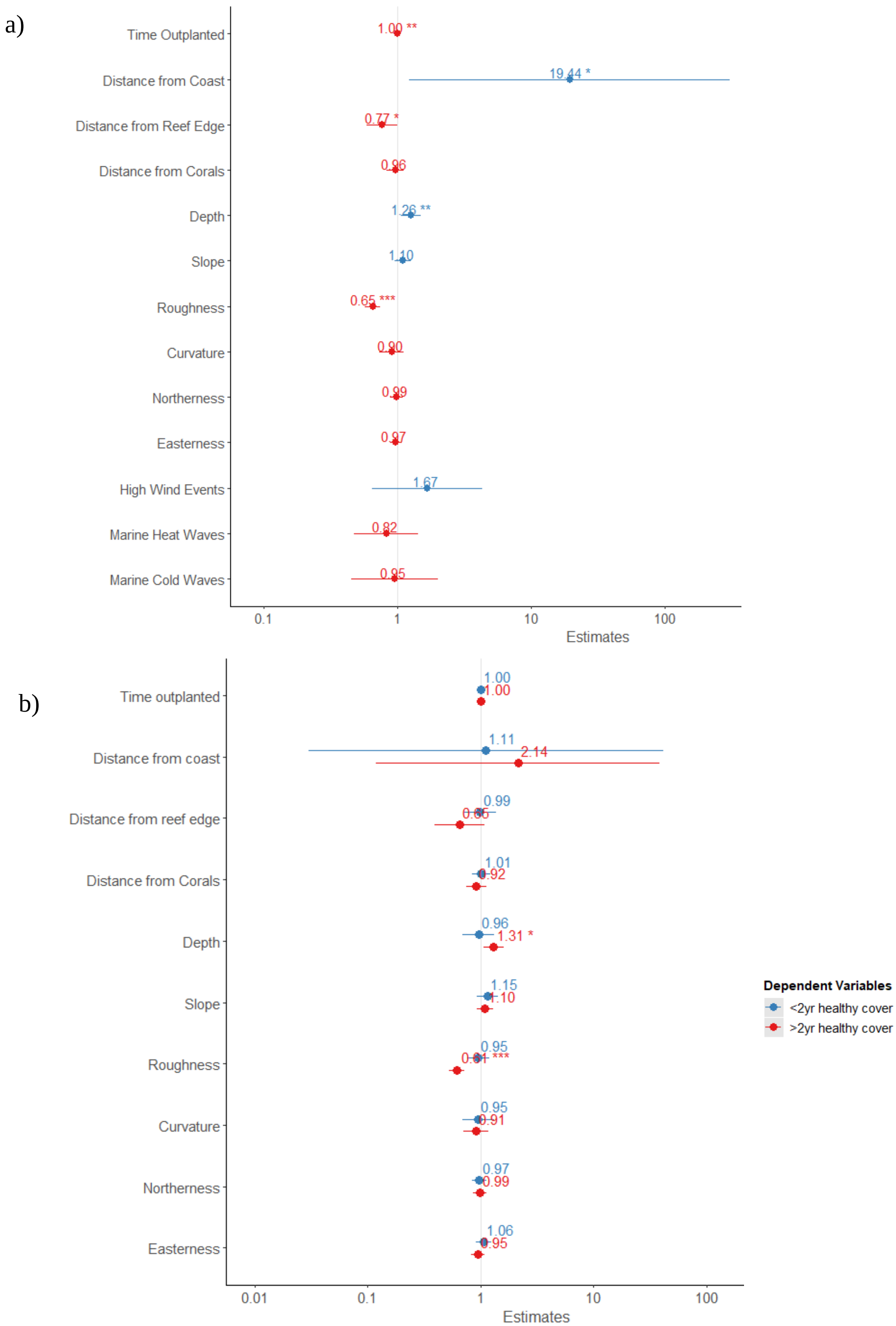

Figure 5: Percent coral healthy tissue model covariate estimates for each covariate for all corals (a) and subset models of young (<2yro) and old (>2yro) (b) corals.

3.2 Healthy and Total Growth Model

Corals experienced total and healthy growth (t-test, $t_t = 22.718$, $p_t < 0.001$; t-test, $t_h = 14.562$, $p_t < 0.001$). Healthy growth averaged 16.1949cm^2/yr (CI: 14.124-18.528 cm^2/yr) and total growth averaged 26.03492 cm^2/yr (CI: 24.188-28.766 cm^2/yr). Healthy (ANOVA, $F_{8, 579} = 6.085$, $p < 0.001$) and total (ANOVA, $F_{8, 579} = 11.29$, $p < 0.001$) growth varied across sites, but did not change over time (GLMM, $z_t = 0.974$, $p_t = 0.33$; GLMM, $z_h = -1.455$, $p_h = 0.145$) (Fig. 6).

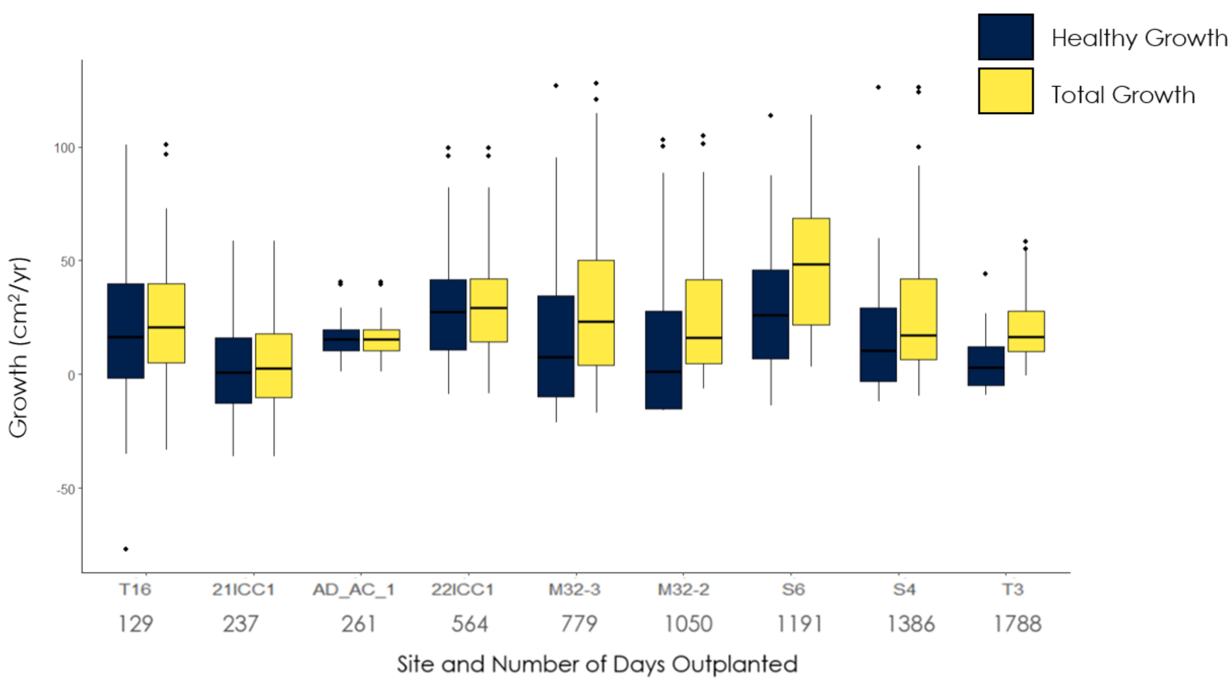

Figure 6: Total and healthy coral growth for all sites.

Total and healthy growth models converged according to the Hessian statistic and had AIC values of 4928.682 and 4955.466, respectively. A number of variables correlated with higher total and healthy coral growth. This include distance from shoreline (GLMM, $z_t = 2.228$,

p_t = 0.026; GLMM, z_h = 2.453, p_h = 0.014), increasing slope (GLMM, z_t = 2.266, p_t = 0.023; GLMM, z_h = 2.565, p_h = 0.010), decreasing roughness (GLMM, z_t = -2.810, p_t = 0.004; GLMM, z_h = -4.224, p_h < 0.001), decreasing curvature (concavity) (GLMM, z_t = -3.842, p_t < 0.001; GLMM, z_h = -3.289, p_h = 0.001), increasing high wind events (GLMM, z_t = 2.030, p_t = 0.042; GLMM, z_h = 2.589, p_h = 0.009) and decreasing marine cold waves (GLMM, z_t = -3.729, p_t < 0.001; GLMM, z_h = -3.160, p_h = 0.0015). Increasing marine heat waves correlated with lower total growth only (GLMM, z = -2.228, p = 0.025) (Fig.7).

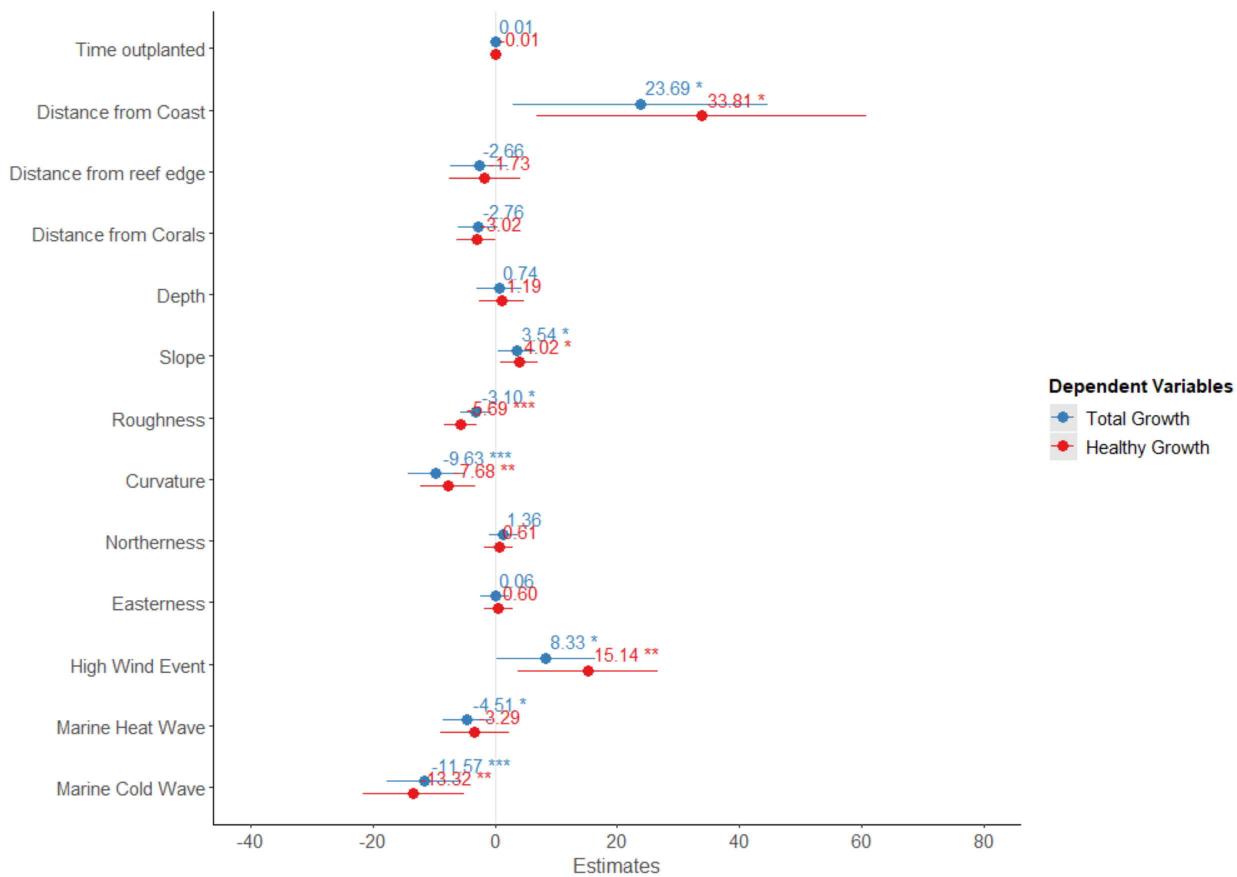

Figure 7: Healthy and total growth model covariate estimates for each covariate for all corals.

Chapter 4: Discussion

4.1 Model Results

4.1.1 Environmental Covariates for Percent Healthy Cover

Overall, the fine-scale models of this study suggest a number of terrain attributes and environmental variables correlate with higher coral percent healthy cover. Model results indicate depth, roughness, distance from the reef edge, and distance from the coast significantly correlate with coral percent healthy cover. Percent healthy cover is a product of where corals are less exposed to disease causing microbes, are more resilient to disease, or where corals are best able to recover from infection (Shore & Caldwell, 2019). All the correlating environmental variables can contribute to these conditions.

Corals within the current study resided six to ten meters deep. Reef restoration, such as those led by Mission Iconic Reef, has focused on the shallow reef crest, reef crest, spur and groove terrain, forereef terrace, and deep reef (*Mission: Iconic Reefs - Carysfort Reef*, n.d.). These sites, apart from the deep reef, range in depth from 0.7m to 10m deep and constitute over 56,000m^2 of restorable area. The model within this study found depth to be correlated with increased percent healthy coral cover. In other studies, depth and turbidity have been shown to be superior when predicting corals afflicted by disease, compared to biotic variables (Williams et al., 2010). This is due to mitigating coral's exposure to ultraviolet radiation and temperature fluctuations, which contribute to bleaching and disease (Asner et al., 2022; Buma et al., 2001; Giraldo-Ospina et al., 2020). Their sensitivity to UV radiation is especially prevalent in the upper 10m of the water column (Buma et al., 2001), making the corals of this study and much of the restorable area restoration groups are outplanting to, within the depth of negative impact. To avoid coral outplants from suffering from such UV radiation and temperature fluctuations, future coral outplanting at shallow water sites should focus on outplanting below 8m deep and should further explore outplanting in deep reefs.

Interestingly, we found decreasing roughness was positively correlated to healthy coral cover, in contrast to larger scale studies. Other studies have shown coral tissue roughness increases micro-turbulences, thereby increasing food uptake (Hearn et al., 2001). Additionally, surrounding roughness would indicate a more complex terrain and has normally associated well with coral resilience (Magel et al., 2019). There are several potential reasons for these unexpected model results. The first is increased surrounding roughness is indicative of higher coral abundance, which may facilitate contact-spread of disease (Burns et al., 2015; Goergen et al., 2019; Shore & Caldwell, 2019). Less surrounding roughness would provide corals with space and water flow to prevent infectious microbes from making contact. Second, a coral in complex terrain, with other corals and a rocky benthic environment with holes for organisms to occupy, would be more attractive for corallivores to populate. Less rough terrain would not be suitable for corallivores to occupy and therefore the *A. cervicornis* outplant would accumulate less tissue lesions for disease to enter (Borland et al., 2021; Montalbetti et al., 2022; Nicolet et al., 2018; Shore & Caldwell, 2019; Williams et al., 2010). Lastly, high terrain roughness and surrounding corals with rough tissue, as aforementioned, results in an increased capacity for the coral to uptake food. This indicates an increased capacity to uptake disease causing microbes (Hearn et al., 2001; Morrow et al., 2022; Shore & Caldwell, 2019). Less terrain and coral roughness surrounding an outplant would decrease micro-turbulence and resulting exposure to infection.

Further research investigating *A. cervicornis* outplanting over a spectrum of habitat complexity and proximity to other infectious corals could help elucidate such inquiries.

Model results of this study show percent healthy coral cover is higher when closer to the reef edge. The reef edge – the interface between the spur and groove terrain – has resulting higher water flow from the sandy groove channels that have been carved from water flow, while remaining higher on the reef spurs which prevent sediment accumulation. HSMs (van Woesik et al., 2020) and coral zonation (Tomascik & Sander, 1987) studies favor corals along moderate flow environments due to positively influencing food availability, mass transfer, and dissolved oxygen content. Higher water flow also reduces stagnant warm water and sediment accumulation (Roberts et al., 1992; van Woesik et al., 2021). These favorable environmental conditions prevent environmental stress which would weaken coral and make them vulnerable to disease. Though these results have not been explicitly evaluated, restoration activities at Mote Marine Lab have increased their efforts on outplanting close to the reef edge, as their observations suggest the location to be favorable for coral outplant success.

The model projected improved coral cover farther from shore, supporting results shown by van Woesik et al., (2020), and can be attributed to reduced exposure to anthropogenic run-off (Golbuu et al., 2011). The corals closer to shore also resided closer to the middle keys, which have shown to be especially poor locations for corals due to the smaller islands causing large tidal channels from Florida Bay (Ginsburg & Shinn, 1995; Harrison et al., 2019; Toth et al., 2019; van Woesik et al., 2021). These tidal channels deliver unfavorable terrestrial material, sediments, and organic matter for coral reef development (Lirman & Fong, 2007).

4.1.2 Environmental Covariates for Total and Healthy Growth

Other than MHW, covariates which were shown to significantly correlate to total growth also significantly related to healthy growth in the same manner and proportion. If corals after being infected with disease would grow differently in different environmental conditions, then results would have been different for the two models. However, since the model results are the same for both total and healthy growth, this indicates that coral needs and optimal conditions for growth did not change after being infected with disease and would relate to healthy growth similarly to total growth. Total and healthy growth give an indication where there is optimal mass transfer and minimal stress. All the correlating environmental variables can contribute to these conditions. Less terrain roughness and increased distance from shore positively correlated with higher total and healthy growth and is likely due to similar reasons as positively associating with percent healthy cover; increased environmental stress supports disease infections and inhibits growth. Additionally, terrain steepness, terrain curvature, and high intensity event are significantly correlated with growth.

While distance from the reef edge was not shown to be significantly correlated with higher growth, higher slope was significantly correlated with higher healthy and total growth. This is likely due to slope indicating the strength of water flow developing contourite features, both causing the sandy grooves and across the coral spurs (Eugene Shinn, 1963; Hernández-Molina et al., 2011). Deeper groove channels are products of stronger water flow, exemplifying that while healthy coral cover benefits from water flow, growth is dependent upon the strength of such water flow providing ample food for mass balance transfer and dissolved oxygen.

Site curvature was relatively flat throughout all the sites. Highly convex coral outplant locations resided on top of large rocks interspersed throughout the site or when overshadowed by sea plumes, sea fans, sea rods, and sea whips. Concave morphology has previously shown negative relations to coral growth due to food depletion occurring faster (Merks et al., 2004), sediment accumulation (Philipp & Fabricius, 2003), and lack of water flow (Sebens et al., 2003). However, at small spatial scales and from a birds-eye perspective for data collection, convex terrain represents unfavorable outplant location. Convex terrain would be vulnerable and exposed locations, or next to encroaching organisms limiting waterflow and competing for resources, thereby reducing mass balance transfer. Outplanted corals in the future should not be outplanted on high on rocks or right next to physical and biological features which can interrupt water flow.

Increased MHW are negatively correlated with total coral growth and increased MCW events negatively correlated with total and healthy growth, according to model results. This is by no means surprising. Marine heat wave events have a long-standing evidential history of negatively influencing coral success (Ainsworth et al., 2020; Asner et al., 2022; Donovan et al., 2021; Foo & Asner, 2020; Hughes et al., 2018; Oliver et al., 2021), and climate projections show marine heat waves are main drivers in inhibiting coral growth (Cantin et al., 2010) and causing coral reef decline (IPCC, 2018). While attention has focused on the effect of MHW over MCW, due to the expected increase in intensity and duration of MHW and decreased prevalence of MCW due to climate change (IPCC, 2018), model results here showed MCW had a greater negative impact on *A. cervicornis* growth than MHW. One of the most severe cold-water events in the Florida Keys on record occurred in 2010 (Colella et al., 2012; Kemp et al., 2016; Lirman et al., 2011) and another in the winter of 1976-1977 (Porter et al., 1981), causing mass mortalities throughout the Florida Reef Tract. *A. cervicornis* and other corals' high vulnerability to cold water events raises concerns over selective breeding and outplanting of heat tolerant corals to combat bleaching (Buerger et al., 2020; Howells et al., 2021). This form of selection may therefore leave reefs more vulnerable to cold wave events.

In addition, the model projected high wind events had a positive effect on coral growth. High wind events have been associated with increased lesions (Goergen et al., 2019), reduced growth (Muko et al., 2013), increase run-off (Riegl et al., 2009), and induce mortality (Goergen et al., 2019). Despite these negative effects, HWEs have been shown to mitigate bleaching through ocean cooling (Carrigan & Puotinen, 2014; Manzello et al., 2007; Page et al., 2021). While HWEs increase breakage, this fragmentation encourages asexual propagation (Lirman, 2000; Lirman et al., 2014). High winds also increase wave action and water flow, benefiting coral growth. High wind events within this study were defined by a wind speed threshold that is lower than in other studies, suggesting the model results could also be a product of including wind events that are not exclusively destructive. While the impact of high wind events on corals should still further explored, the findings of this study show they are far less of a concern in comparison to high intensity thermal and cold wave events.

4.1.3 Young vs Old Coral

A. cervicornis coral restoration and monitoring has thus far focused primarily on initial coral health, rarely exceeding one year of monitoring (Fox et al., 2019). Survivorship and resilience to disease is highest in the first few years following outplanting (Ware et al., 2020). In the limited studies focused on *A. cervicornis* after two years, growth and survivorship decreased (Ware et al., 2020). Corals in the present study did not exhibit any decrease in growth trends after two years, but did decrease in percent healthy cover, emphasizing the importance of utilizing corals outplanted for longer than two years when developing habitat suitability models for outplant survivorship and healthy cover. In contrast to results for percent healthy cover for all corals, the model for corals outplanted for less than two years was unable to identify correlating terrain attributes which positively related to percent healthy cover. A possible reason for the decline in healthy coral cover after two years of ouplanting may be due to the onset of spawning. *A. cervicornis* starts spawning around 2 years of age, which likely diverts their energetic resources from fighting infection to reproduction and growth (REEFocus, 2020; Lirman, 2000; Omori, 2019). Overall, these salient results emphasize the importance of long-term monitoring when informing outplant location considerations to build resilient and enduring *A. cervicornis* reefs.

Within this study growth did not change with time outplanted, but it is important to acknowledge the scope of this study did not include monitoring the same corals over time to establish growth trends. Further studies should monitor coral outplant growth year to year, since outplantation. Many studies presume growth continues throughout *A. cervicornis* lifetime and has utilized growth as a proxy for successful coral communities of wild *A. cervicornis* populations of indeterminate age (Jones, 1973; Goergen et al., 2019; Drury et al., 2019; Weil et al., 2020). Despite this, coral outplants are known to perform differently than wild corals (Lirman et al., 2010; Omori, 2019) and growth models of *A. cervicornis* outplants show a decrease in growth over time (Muko et al., 2013; Ware et al., 2020). While this study aimed to further understand coral outplant growth over time, such comprehensive findings will not be elucidated until coral outplant growth is continuously and comprehensively monitored into the long-term.

Within the present study five of the nine sites which had corals outplanted for more than two years all resided within the lower Florida Reef Tract, requiring the exploration of older outplanted corals in more diverse and spatially distant locations. Of the five sites with older corals, the two within Sand Key exhibited the highest median healthy coral cover, but the corals at Eastern Dry Rock exhibited the lowest median healthy coral cover, indicating that Sand Key's healthy coral cover is likely not wholly attributed to the protection provided by the site residing within a national marine sanctuary.

4.1.4 Paradox of Coral Restoration

Model results of curvature and roughness convey the reoccurring issue with coral restoration; often coral outplanting results in unfavorable environmental conditions for optimal coral growth and survivorship. Creating large reef-building coral thickets within the Florida Reef Tract increases coral vulnerability to density induced disease spread (Anderson & May, 1979; Shore & Caldwell, 2019). Reef-building coral thickets will increase corallivore presence which populates the reefs and cause coral lesions (Koval et al., 2020; Montalbetti et al., 2022). Mass coral thickets decrease water flow penetration into the thickets and result in water flowing across the top, thereby reducing flow regimes and mass flux at the base of the coral (Reidenbach et al., 2007; Stocking et al., 2016). In less rough and convex terrain *A. cervicornis* had higher growth and healthy cover trends, yet the coral itself has rough and convex morphology, resulting in the coral building unfavorable terrain. There are possible actions that may circumvent the dilemma. One involves withholding corals from outplantation until several years of age, so that sexually reproducing outplants may immediately start recruitment and thereby increase genetic diversity. In the interest of developing self-sustaining coral populations, a second focus is to increase the adaptive potential of outplants to be more resilient to disease and mass flux in the long-term and when starting sexual reproduction.

4.2 Working with Restoration Groups

4.2.1 Restoration Group Capabilities When Developing HSM

Similar to the end goals of coral restoration (building complex and biodiverse habitats can result in environmental conditions which can inhibit optimal coral success) coral outplanting and monitoring capabilities can often stand at odds with maximizing restoration success. Model results within this study and in other studies have shown the future of suitable habitats for coral growth and healthy cover in the long-term will occur primarily in deeper waters (at least below 15m deep) (Giraldo-Ospina et al., 2020) and farther away from the coast (Golbuu et al., 2011). Deeper waters will become an especially important refuge to corals due to mitigating MHW (Giraldo-Ospina et al., 2020; Harrison et al., 2019) and MCW (Porter et al., 1981) effects. Yet, these locations are especially hard for restoration groups to regularly access and monitor. More effort should be made to work together with restoration groups to develop HSMs which identify suitable sites useful to coastal managers and groups that are actively restoring coral. While restoration groups should prioritize outplanting to the deeper parts of accessible sites farther from the coast, efforts should be made to optimize outplanting and monitoring potential to more distant locations. Opportunities to survey coral reef growth and health more efficiently using remote sensing techniques should be explored as it can increase monitoring capabilities. Potential applications include ICESat-2 satellite monitoring, multibeam, and unmanned aerial surveillance. Complimenting these survey methods with HSMs and deep learning coral detection can provide more accessible monitoring of corals in environments which may be difficult to monitor recurringly *in-situ*.

4.2.2 Importance of Long-term Monitoring

Though growth trends did not change over time, percent healthy cover was greater in the first two years of outplanting and then significantly declined after two years. While this emphasizes the importance of coral monitoring corals across multiple years, it also displays the importance of monitoring multiple measures of coral success and keeping measurement methods consistent. Coral restoration and monitoring suffers from unstandardized methods of determining and measuring corals success (Boström-Einarsson et al., 2020). Often total lateral extension (TLE), the total amount of growth *A. cervicornis* nodes exhibit, is used as a measure for growth in the short-term. This form of monitoring, however, becomes unfeasible when *A. cervicornis* becomes too large with too many branches that can reasonably be measured. This issue is compounded by individual corals fusing with each other when coming into physical contact. As a result, long-term coral outplants are often measured differently (number of nodes, total skeletal cover, maximum skeletal width, maximum skeletal height, etc.) (Boström-Einarsson et al., 2020; Drury et al., 2019; Larcom et al., 2014; Lartaud et al., 2016) than corals outplanted for less than a year. Additionally, corals may be evaluated using models (Muko et al., 2013; Ware et al., 2020), such as linear, logistic, or Gompertz growth model, in order to analyze growth trends, making comparisons misrepresentative.

Monitoring corals should be consistent across time and given the greater interest in using remote sensing technologies for coral monitoring purposes, it would be beneficial to target measurement methodologies that can be used and compared across monitoring platforms. TLE is only feasible in the short term and *in-situ*. Height measurements, while quantifiable across time, can only be taken *in-situ*. Theoretically these measurements can be attained from stereo-imagery photogrammetry derived 3D terrain models, though the models themselves can suffer from inconsistent quality (Appendix 1) and therefore variable measurements. Measurements of cover size or maximum skeletal width are viable *in-situ*, from photography (scale bar provided), and from stereo-imagery photogrammetry (Appendix 2).

4.2.3 Importance of Fine-scale

Roughness and curvature terrain attributes were highly variable in the fine-scale and provided unique insight into minute environmental conditions which influenced coral healthy cover and growth. Qualitative observations of model results showed the high roughness and convexity which negatively correlated with coral success could be primarily attributed to encroaching soft coral and rocks. This fine-scale insight, which would be neglected in coarse resolution HSMs, exemplifies higher resolution capabilities to bridge the gap from broader environmental conditions to minute and morphological conditions which contribute to organismal success (Stocking et al., 2016). Though the majority of current HSMs use broader environmental conditions and thereby develop insight into broad-ranging organismal relations with environmental conditions, fine-scale data resolutions have been neglected in model development and have left an opportunity to explore comprehensive morphological relations between organisms and their environment. This study aimed to initiate such an investigation.

4.3 Terrain Attribute Variability

In the process of developing such models, several pitfalls were revealed, unique to these models. Often in HSMs, covariate data resolutions are larger than the organism, resulting in covariate values being pulled directly from the raster cell which the organism occupies. Fine-scale spatial data thereby relies on the calculation of associating values. In the case of this study, this meant calculating associating terrain attributes with each individual coral. Terrain attributes and accuracy are resolution dependent (Deng et al., 2007; GAO, J., 1997; Qiang et al., 2021; Rengstorf et al., 2012). This means a single coral could have different values of slope, aspect, curvature, and so on depending on the resolution of the spatial data. Terrain attributes are also cell calculation window dependent (Iwahashi et al., 2012; Misiuk et al., 2021), which refers to how many of the surrounding cells are utilized when calculating a single cell's value. Terrain attributes also have the capacity to be data collection platform dependent (Deliry & Avdan, 2021; Rowley et al., 2020). Within the current study DEMs were developed using *in-situ* stereo imagery photogrammetry, but DEMs can also be developed through UAS photogrammetry, multi-beam, and ICESat-2 (Slocum et al., 2019). Terrain attributes also have many calculation forms (Deng et al., 2007; Fukunaga et al., 2019; Pygas et al., 2020; Young et al., 2017). Curvature for example within ArcGIS Pro can be calculated as planar curvature, profile curvature, tangential curvature, geodesic torsion, Casorati curvature, and Gaussian curvature. Resulting calculations can have significantly different values from each other (Blaga, 2019). Terrain attributes can also be calculated within ArcGIS Pro by fitting a plane to a cell or by fitting a surface to a cell, which better calculates values in the fine-scale (Kopp, 2/21). These calculation forms can result in different values for some terrain attributes like slope and curvature (Blaga, 2019; Deng et al., 2007; Appendix 3), while not affecting other terrain attributes as much (Deng et al., 2007; Appendix 4). These differences in terrain attribute values result in different HSM results (Rengstorf et al., 2012; Appendix 5 & 6). The current study replicated terrain attribute calculation methods that have been used in other studies, or to yield values observable by the human eye (Burns et al., 2015; Burns et al., 2019). Future validation of terrain attributes to *in-situ* measurable terrain values and HSM results should occur across resolution, cell calculation windows, data collection platforms, and calculation methods.

Chapter 5: Conclusion

In the wake of mounting climate change induced stressors, coral reefs around the world are dramatically decreasing, including the important stony reef-building coral *Acropora cervicornis*. Coral outplanting has been a primary form of restoration, but current habitat suitability models of wild *A. cervicornis* populations have provided broad and imprecise recommendations for outplantation. With the use of Structure-from-Motion fine-scale, site specific, digital elevation models can be created to support habitat suitability model development in order to predict coral health variability within outplant sites. The purpose of this study was to create fine-scale habitat suitability models to determine which within site seafloor terrain attributes contribute to growth and percent healthy cover of outplanted *A. cervicornis*.

Overall, those corals farther from the coast, in deeper waters, near the reef edge, and in less rough terrain have better healthy cover. Healthy cover is a product of *A. cervicornis* vulnerability to disease, which can be induced by abiotic and biotic stress and increased contact with disease. Corals farther from the coast are less exposed to stress inducing anthropogenic runoff. Deeper waters help deter infection by mitigating temperature fluctuations and UV radiation, which weaken corals and leave them vulnerable to disease. Corals would be less vulnerable to disease near the reef edge due to higher water flow that prevents water from becoming stagnant, hotspots for disease causing microbes. Lastly, rough terrain could have multiple negative effects on corals which cause disease to spread. This includes contact induced spread of disease with other corals, increasing microturbulences, and increasing corallivore presence and resulting lesions on coral tissue.

Like the model output for healthy cover, total and healthy growth were correlated with distance from the coast and roughness, likely because of less pollutants, less opportunities for infection, and less competition for food. Terrain curvature and slope also influenced total and healthy growth. Like roughness, concave environments would represent environments where the coral is provided space immediately surrounding it, as opposed to organisms with convex morphology that inhibit water flow and compete for resources. Steep terrain is highly correlated with increased growth as the gradient represents the strength of within-site high water flow, extending beyond water flow information provided by distance from the reef edge, which delivers more dissolved oxygen and food to the coral than low flow environments.

Cumulatively, the results of this study demonstrate how Structure-from-Motion models can be used in restoration activities. Further, they emphasize the importance of fine-scale monitoring coral reefs in the long-term, as well as the need to utilize diverse survey techniques, including ICESat-2 satellite monitoring, multibeam, and unmanned aerial surveillance. The nature of the study's habitat suitability models utilizing high resolution digital elevation models at the millimeter scale provided insight into how terrain variables at scales relevant to the individual coral influence coral health. This would not be captured by other habitat suitability models, which use spatial resolutions of seafloor data several orders of magnitude larger. The focus of this study using habitat suitability models of corals less than and greater than two years old helped to provide insight into environmental conditions which promote healthy coral cover, which would not otherwise have been evident if using corals that had only been outplanted for a year. This emphasizes the necessity for coral reef managers to consider beyond the initial two-year conditions when outplanting corals. The importance of deeper and more distant environmental refuges for long-term coral health necessitates developing approaches utilizing remote sensing platforms for coral monitoring in waters that may be too deep for satellite observation. This will support more efficient and effective coral outplanting to environments which will be more resilient to climactic changes in the decades to come.

Appendix A: Three-Dimension Terrain Model Quality Variability

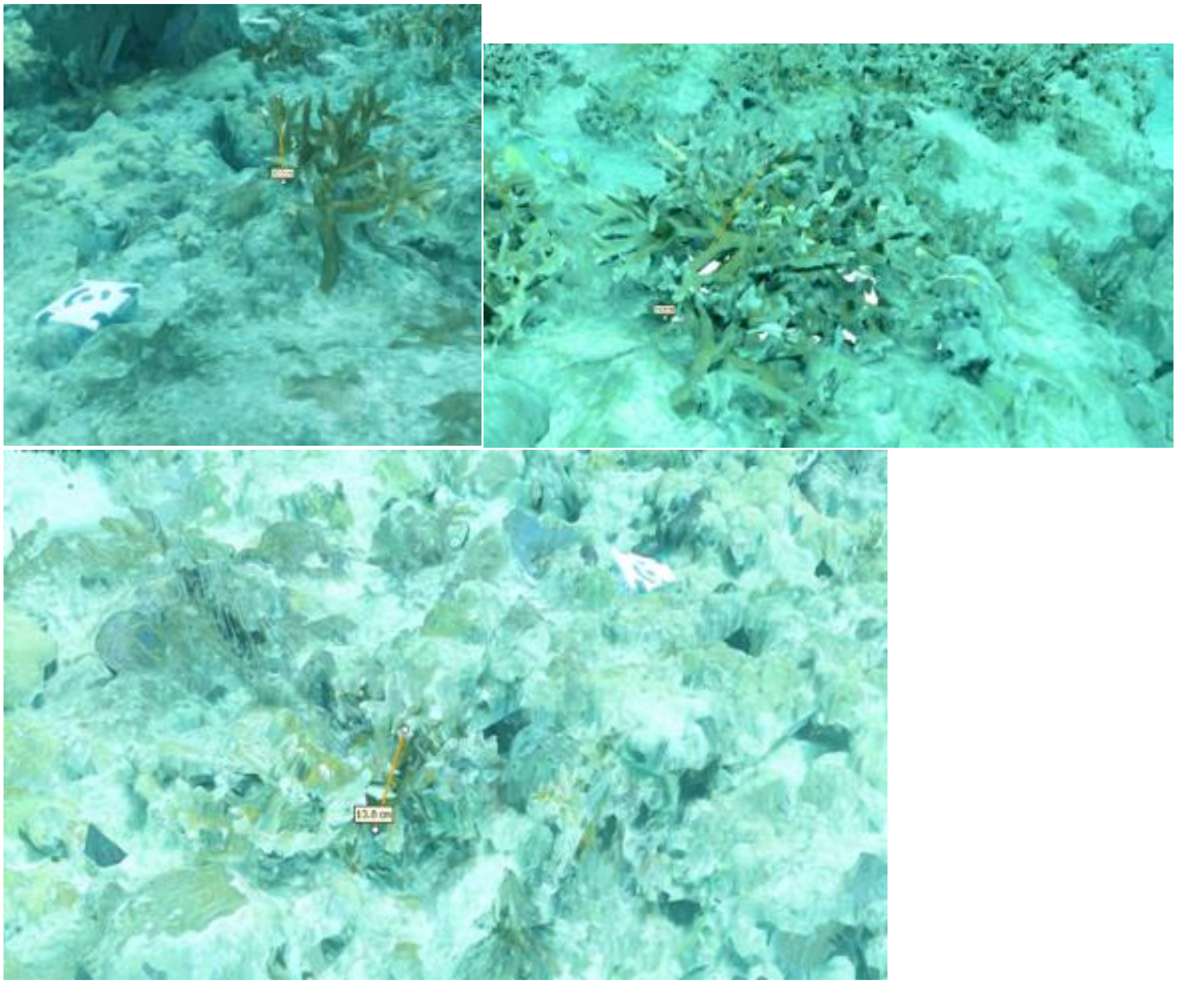

Figure A1: Three-dimension terrain models had variable image quality due to camera type, photogrammetry image blurriness, light quality, turbidity, and model development procedure. Some 3D models had clear imagery of the staghorn coral (a), identifiable but less clear imagery of the coral (b), or extremely difficult to identify coral (c) making collecting height measurements difficult to validate.

Appendix B: Orthomosaic Measurement Validation

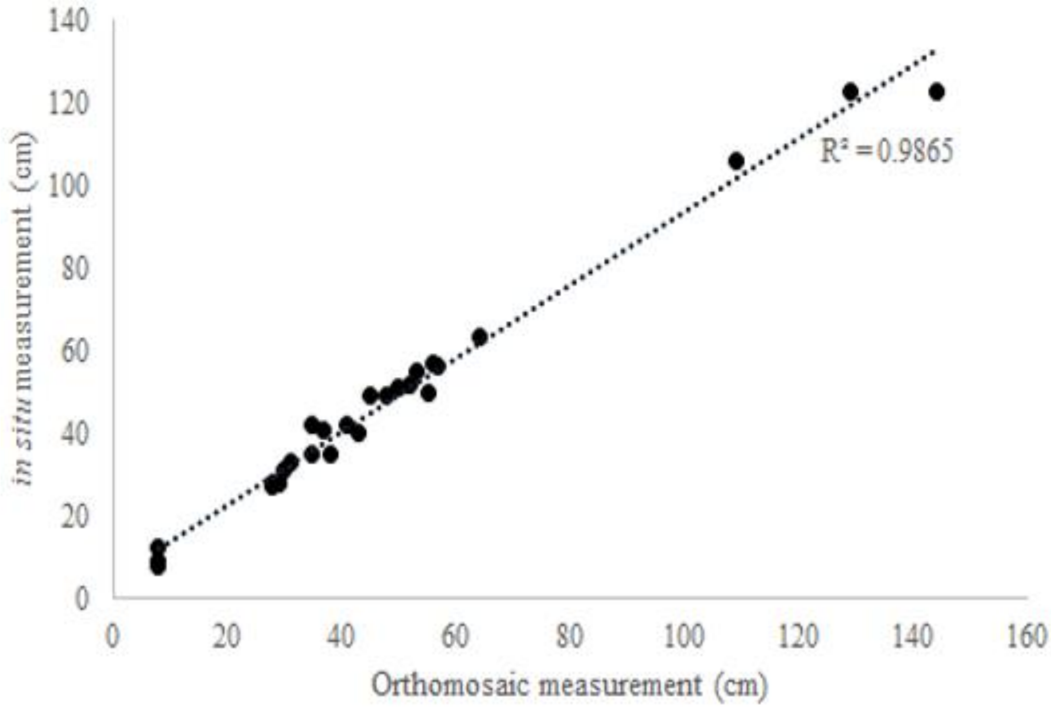

Figure B1: Maximum skeletal length was measured *in-situ* and compared to orthomosaic measurements. If photogrammetry processing occurred correctly, measurements were highly accurate compared to real world measurements (R^2=0.9865), but at times processing and orthomosaic development was hindered by poor data management.

Appendix C: Slope and Curvature Terrain Attribute Variability

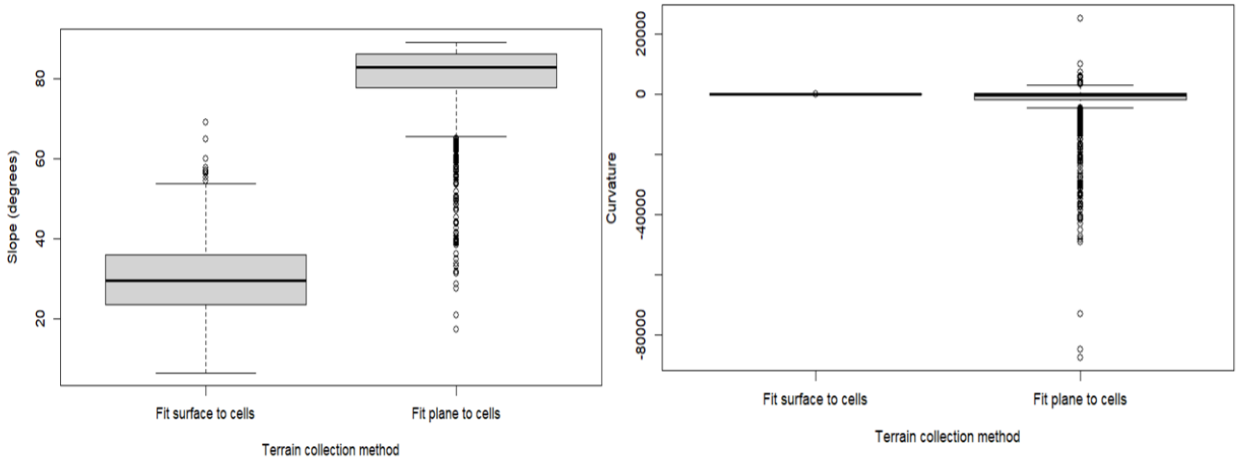

Figure C1: Terrain attributes resulted in very different values depending on if the Surface Information and Curvature tool were used to collect slope and curvature values, respectively, as opposed to the Surface Parameter tool. The Surface Parameter tool fits a surface to cells to calculate values, instead of previous tools which fit a plane to cells.

Appendix D: Northerness and Easterness Terrain Attribute Variability

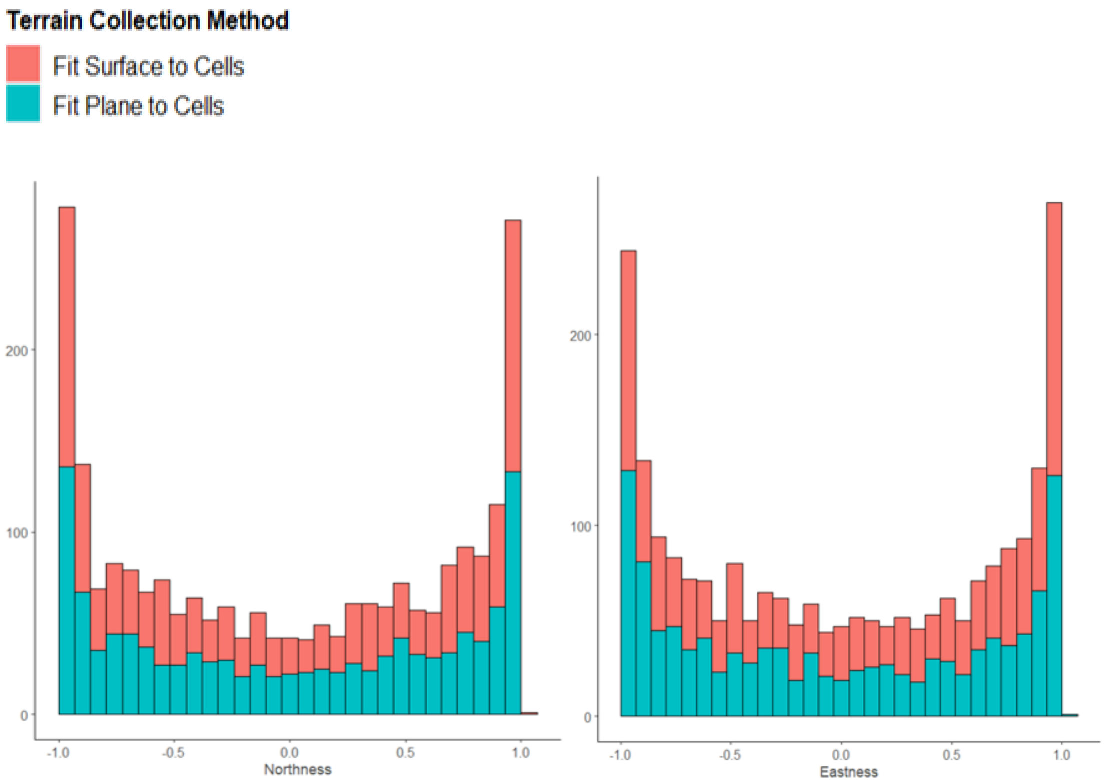

Figure D1: The Aspect tool, which fits a plane to a cell, and the Surface Parameter tool, which fits a surface to a cell, results in similar values of Northerness and Easterness.

Appendix E: Young and Old Coral Percent Healthy Cover Model Result Variability

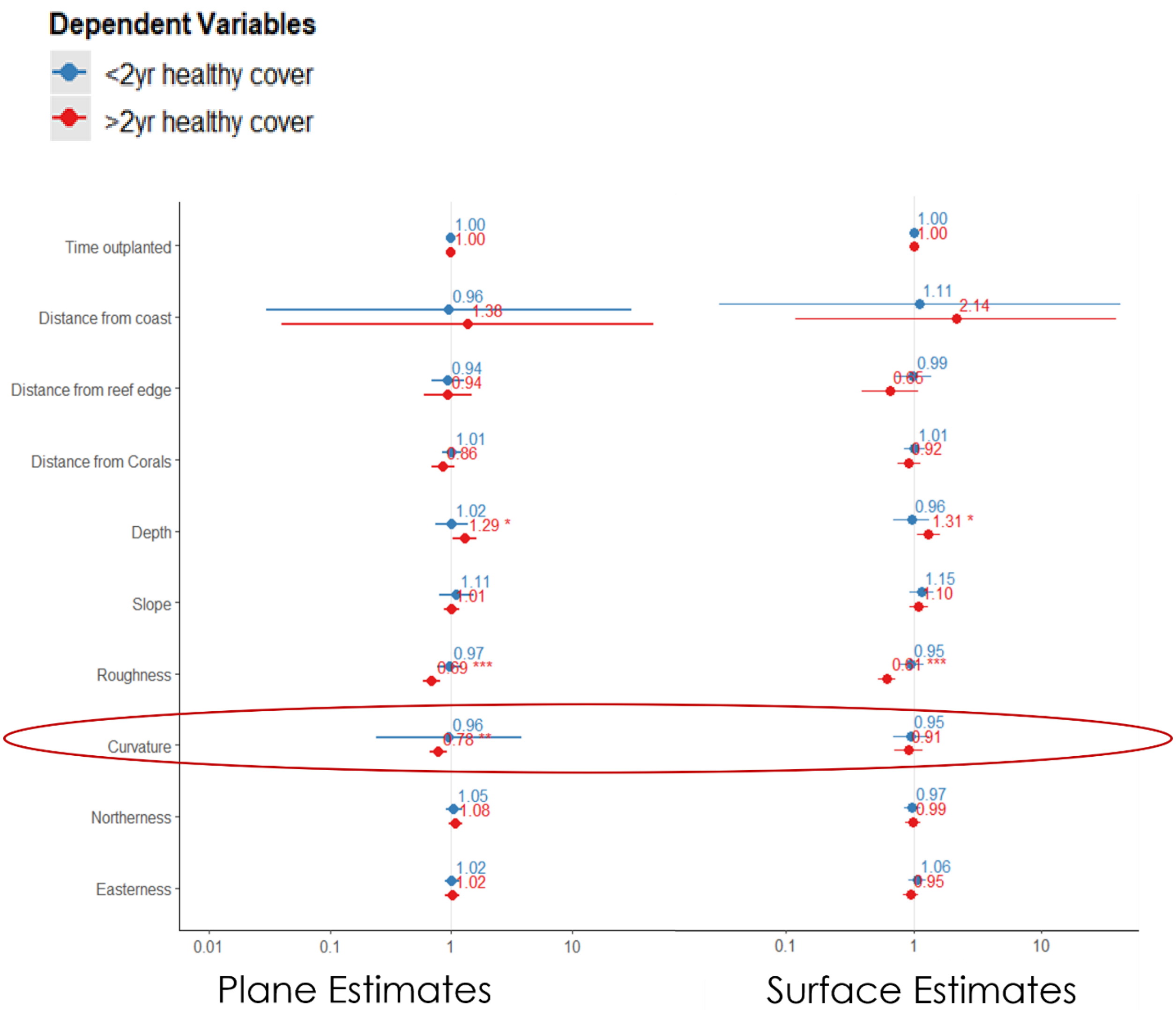

Figure E1: Model results for percent healthy cover, using terrain attributes which fit a plane to a cell vs. a surface to a cell for slope, curvature, Northerness, and Easterness result in different model results with covariate significance. When fitting a plane to a cell, curvature is significantly correlated with healthy coral cover for corals older than two years old.

Appendix F: Coral Growth Model Result Variability

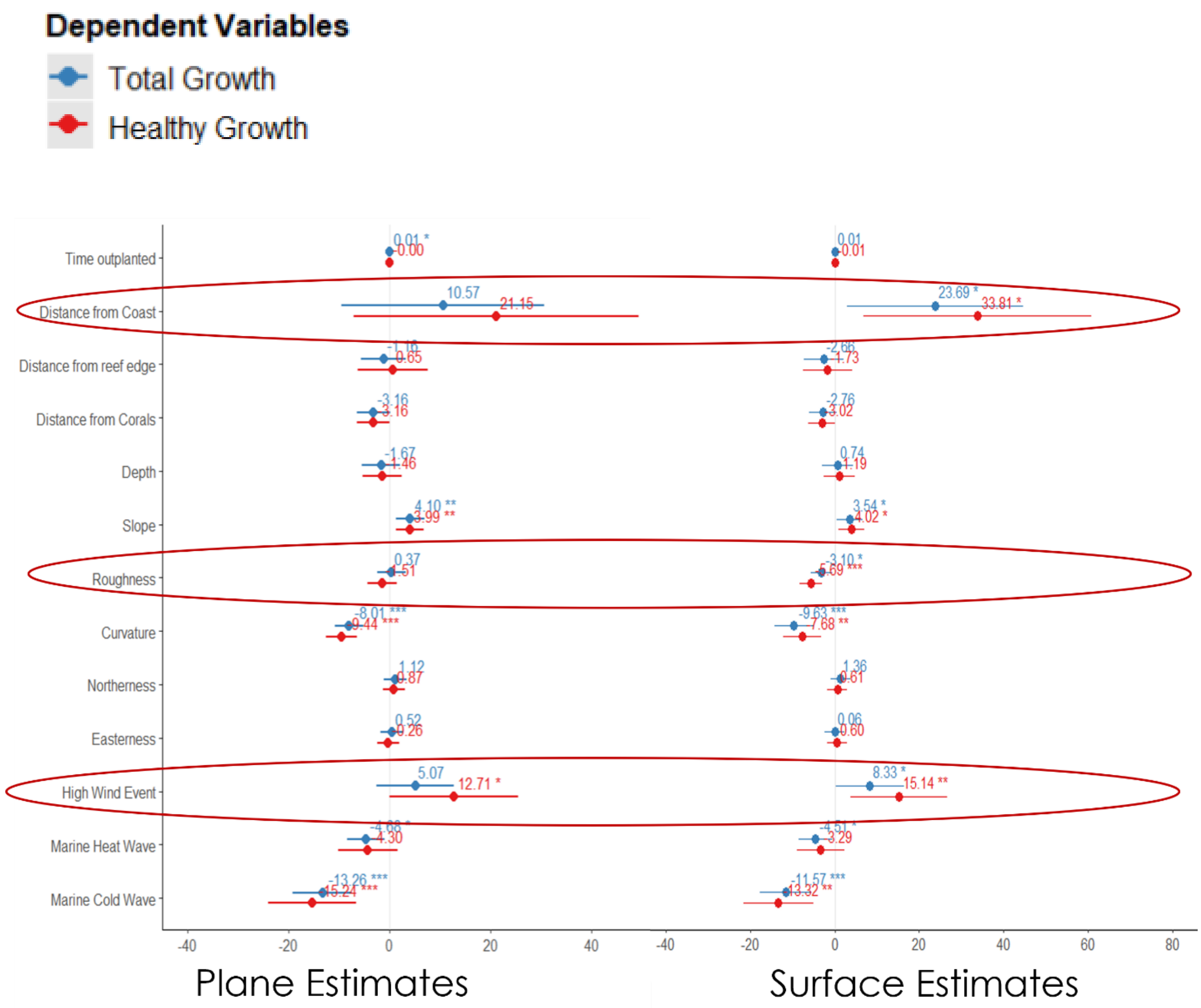

Figure F1: Model results for total and healthy growth, using terrain attributes which fit a plane to a cell vs. a surface to a cell for slope, curvature, Northerness, and Easterness result in different model results with covariate significance. When fitting a plane to a cell, distance from coast, terrain roughness, and HWE for total growth are no longer significantly correlated.

Appendix G: R Code

```
# Import Data ---------------------------------------------------------------
library(readxl)
setwd("Z:/Glenna/Thesis/Coral")
Coral_cover <- read_excel("Data/Data.xlsx")
View(Coral_cover)

# Variables ---------------------------------------------------------------
### Format Coral Data ###
# Exclude Coral Fragments and Wild Corals
corals <- subset(Coral_cover, CoralID!="Wild")
corals <- subset(corals, CoralID!="Frag")
corals <- subset(corals, CoralID!="Ignore")

# Coral Cover per Coral in Aggregates
coral_number <- as.numeric(corals$CoralID)
final_healthy_cover <- 10000*((corals$Healthy_cover)/coral_number) #convert m^2 to cm^2
final_total_cover <- 10000*((corals$Total_cover)/coral_number) #convert m^2 to cm^2
initial_cover <- 10000*(corals$initial_size) #convert m^2 to cm^2

### Response Variables ###
# Percent of Coral Cover with Healthy Tissue (%)
perc_healthy_cover <- (final_healthy_cover / final_total_cover)
# Transform Y = 0 and Y = 1 so 0.001< Y <0.999 and beta distribution can be used
perc_healthy_cover <- ifelse(perc_healthy_cover>0.999, 0.999, perc_healthy_cover)
perc_healthy_cover <- ifelse(perc_healthy_cover<0.001, 0.001, perc_healthy_cover)

# Healthy Growth (cm^2)
healthy_growth <- ((final_healthy_cover)-
(initial_cover))/(as.numeric(difftime(corals$date_collected,corals$date_outplanted,unit="weeks"
))/52.25)

# Total Growth (cm^2)
total_growth <- ((final_total_cover)-
(initial_cover))/(as.numeric(difftime(corals$date_collected,corals$date_outplanted,unit="weeks"
))/52.25)

### Covariates ###
# Random Effect Covariate
Site <- corals$Site
```

```
Site <- as.factor(Site)

# Environmental Characteristics
time <- corals$time_outplanted
CoastDist <- scale(corals$NearCoast)[,1]
ReefDist <- scale(as.numeric(corals$NearReef))[,1]
CoralDist <- scale(corals$NearCoral)[,1]

# Bathymetry Terrain Attributes
Depth <- scale(abs(corals$Depth))[,1]
Slope <- scale(corals$Slope)[,1]
Roughness <- scale(corals$Roughness)[,1]
Curvature <- scale(corals$Curvature)[,1]
Northerness <- scale(cos(corals$Aspect))[,1]
Easterness <- scale(sin(corals$Aspect))[,1]

# High Intensity Events
hwe <- scale(corals$hwe)[,1]
mhw <- scale(corals$mhw)[,1]
mcw <- scale(corals$mcw)[,1]

### Model Matrix for Model Argument "data = " ###
modelmatrix <- as.data.frame(cbind(perc_healthy_cover, healthy_growth, total_growth,
                    time, CoastDist, ReefDist, CoralDist,
                    Depth, Slope, Roughness, Curvature, Northerness, Easterness,
                    hwe, mhw, mcw,
                    Site))
library(openxlsx)
write.xlsx(modelmatrix,'Data/model_matrix.xlsx', colNames = TRUE)

# Covariance -----------------------------------------------------------
### Import Library ###
library(corrplot)

### Make Correlation Plot ###
variables <- subset(modelmatrix, select = c(time, CoastDist, ReefDist, CoralDist,
                         Depth, Slope, Curvature, Roughness, Northerness, Easterness,
                         hwe, mhw, mcw),
            na.rm=TRUE)
variables <- data.matrix(variables)
variables <- cor(variables, use = "pairwise.complete.obs")
```

```
corrplot(variables, method = "number")

# Percent Healthy Cover Model ----------------------------------------------------------------
### Model ###
library("glmmTMB")
perc_healthy_cover_model <- glmmTMB(perc_healthy_cover
                                    ~ time + CoastDist + ReefDist + CoralDist
                                    + Depth + Slope + Roughness + Curvature
                                    + Northerness + Easterness
                                    + hwe + mhw + mcw + (1|Site),
                                    family = beta_family(), data = modelmatrix)

### Diagnostics ###
library(performance)
check_model(perc_healthy_cover_model)
AIC(perc_healthy_cover_model)

### Results ###
summary(perc_healthy_cover_model)
confint(perc_healthy_cover_model)

### Visualization Plot ###
library(sjPlot)
library(ggplot2)
set_theme(base = theme_classic())
plot_model(perc_healthy_cover_model, show.values=TRUE, show.p=TRUE,
        title = (""),
        axis.labels = c("Marine Cold Waves", "Marine Heat Waves", "High Wind Events",
"Easterness", "Northerness", "Curvature", "Roughness", "Slope", "Depth", "Distance from
Corals", "Distance from Reef Edge", "Distance from Coast", "Time Outplanted"))

tab_model(perc_healthy_cover_model, show.se  = "TRUE")

# Young vs Old Percent Healthy Cover ------------------------------------------
### ANOVA of Coral Cover Across Sites ###
perc_healthy_cover_anova <- aov(perc_healthy_cover~as.factor(time), data=modelmatrix)
summary(perc_healthy_cover_anova)
TukeyHSD(perc_healthy_cover_anova)
```

```
### Define Young and Old Corals ###
young_corals <- as.data.frame(subset(modelmatrix, time<730))
old_corals <- as.data.frame(subset(modelmatrix, time>730))

### Correlation Matrix for Young Coral ###
library(corrplot)
variables <- subset(young_corals, select = c(time, CoastDist, ReefDist, CoralDist,
                                            Depth, Slope, Curvature, Roughness, Northerness, Easterness,
                                            hwe, mhw, mcw),
                    na.rm=TRUE)
variables <- data.matrix(variables)
variables <- cor(variables, use = "pairwise.complete.obs")
corrplot(variables, method = "number", title = "Young corals")
#remove intensity_hwe, duration_mhw, duration_mcw

### Young Coral Model ###
library("glmmTMB")
young_perc_healthy_cover_model <- glmmTMB(perc_healthy_cover
                                          ~ time + CoastDist + ReefDist + CoralDist
                                          + Depth + Slope + Roughness + Curvature
                                          + Northerness + Easterness
                                          + (1|Site),
                                          family = beta_family(), data = young_corals)

### Correlation Matrix for Old Coral ###
library(corrplot)
variables <- subset(old_corals, select = c(time, CoastDist, ReefDist, CoralDist,
                                          Depth, Slope, Curvature, Roughness, Northerness, Easterness,
                                          hwe, mhw, mcw),
                    na.rm=TRUE)
variables <- data.matrix(variables)
variables <- cor(variables, use = "pairwise.complete.obs")
corrplot(variables, method = "number")
#remove intensity_hwe, duration_mhw, duration_mcw

### Old Coral Model ###
old_perc_healthy_cover_model <- glmmTMB(perc_healthy_cover
                                        ~ time + CoastDist + ReefDist + CoralDist
                                        + Depth + Slope + Roughness + Curvature + Northerness + Easterness
```

```
                  + (1|Site),
                  family = beta_family(), data = old_corals)

### Diagnostics ###
library(performance)
check_model(young_perc_healthy_cover_model)
AIC(young_perc_healthy_cover_model)
check_model(old_perc_healthy_cover_model)
AIC(old_perc_healthy_cover_model)

### Results ###
summary(young_perc_healthy_cover_model)
confint(young_perc_healthy_cover_model)
summary(old_perc_healthy_cover_model)
confint(old_perc_healthy_cover_model)

### Visualization Plot ###
library(sjPlot)
library(ggplot2)
set_theme(base = theme_classic())
plot_models(young_perc_healthy_cover_model,old_perc_healthy_cover_model,
show.values=TRUE, show.p=TRUE,
        m.labels = c("<2yr healthy cover", ">2yr healthy cover"),
        axis.labels = c("Easterness", "Northerness", "Curvature", "Roughness", "Slope", "Depth",
"Distance from Reef Edge", "Distance from Coast", "Time Outplanted"))
tab_model(young_perc_healthy_cover_model, show.se  = "TRUE")
tab_model(old_perc_healthy_cover_model, show.se = "TRUE")

# Health Growth Model -----------------------------------------------------
### Model ###
library(glmmTMB)
healthy_growth_model <- glmmTMB(healthy_growth
                  ~ time + CoastDist + ReefDist + CoralDist
                  + Depth + Slope + Roughness + Curvature
                  + Northerness + Easterness
                  + hwe + mhw + mcw + (1|Site),
                  family = gaussian(), data = modelmatrix)
#check convergence
isTRUE(healthy_growth_model$sdr$pdHess)
```

```
### Diagnostics ###
library(performance)
check_model(healthy_growth_model)
AIC(healthy_growth_model)

### Results ###
summary(healthy_growth_model)
confint(healthy_growth_model)

### Visualization Plot ###
library(sjPlot)
library(ggplot2)
plot_model(healthy_growth_model, show.values=TRUE, show.p=TRUE,)
tab_model(healthy_growth_model, show.se  = "TRUE")

# Total Growth Model -----------------------------------------------------------
### Model ###
library(glmmTMB)
total_growth_model <- glmmTMB(total_growth
                    ~ time + CoastDist + ReefDist + CoralDist
                    + Depth + Slope + Roughness + Curvature
                    + Northerness + Easterness
                    + hwe + mhw + mcw + (1|Site),
                    family = gaussian(), data = modelmatrix)
#check convergence
isTRUE(total_growth_model$sdr$pdHess)

### Diagnostics ###
library(performance)
check_model(total_growth_model)
AIC(total_growth_model)

### Results ###
summary(total_growth_model)
confint(total_growth_model)

### Visualization Plot ###
library(sjPlot)
library(ggplot2)
plot_model(total_growth_model, show.values=TRUE, show.p=TRUE)
```

```
tab_model(total_growth_model, show.se  = "TRUE")

# Healthy and Total -----------------------------------------------------
### ANOVA of Healthy Growth Across Sites ###
healthy_growth_anova <- aov(healthy_growth~as.factor(Site), data=modelmatrix)
summary(healthy_growth_anova)
TukeyHSD(healthy_growth_anova)

### ANOVA of Total Growth Across Sites ###
total_growth_anova <- aov(total_growth~as.factor(Site), data=modelmatrix)
summary(total_growth_anova)
TukeyHSD(total_growth_anova)

### Healthy Growth T-Test ###
t.test(healthy_growth, mu=0, alternative = ("two.sided"))

### Total Growth T-Test ###
t.test(total_growth, mu=0, alternative = ("two.sided"))

### Visualization Plots ###
library(sjPlot)
library(ggplot2)
set_theme(base = theme_classic())
plot_models(total_growth_model,
        healthy_growth_model,
        show.values = TRUE,
        show.p = TRUE,
        m.labels = c("Total Growth", "Healthy Growth"),
        axis.labels = c("Marine Cold Wave", "Marine Heat Wave", "High Wind Event",
"Easterness", "Northerness", "Curvature", "Roughness", "Slope", "Depth", "Distance from
Corals", "Distance from Reef Edge", "Distance from Coast", "Time Outplanted"))
```

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