TEMPORAL EFFECTIVENESS OF BIODIVERSITY SURROGATES IN CORAL REEFS IN THE BRITISH VIRGIN ISLANDS

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# ABSTRACT

Taxonomic diversity on coral reefs has declined due to anthropogenic stressors. These declines have motivated monitoring programs to estimate species richness for major taxonomic groups: fish and corals. Due to logistical challenges of species identification, there have been efforts attempting to estimate species richness on reefs using landscape features as surrogates, simple indicators that provide an estimate of a target component of biodiversity, often referred to more simply as a target. Many of these efforts are limited in spatial or temporal scope, focus on rugosity and coral cover as predictors, and use coral and fish richnesses as proxies for total species richness. Here we examine how top surrogate-target relationships vary over 27 years and across 8 study sites. We also examine whether frequently measured landscape features of reefs can serve as reliable surrogates for sponge richness. Finally, this study is one of the first to investigate the ability of sponge cover to predict richness of dominant taxonomic groups on coral reefs. This study provides additional support to the idea that surrogate-target relationships should be assessed over space and time because it can provide insight into these relationships and how the ecosystem changes. We also show that including sponges in monitoring studies may provide a broader understanding of how biodiversity is changing on reefs.

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# DEDICATION

This thesis is dedicated to my loving mother, Teresa M. Keefner, my support in all things that led me to complete this work and the woman who taught me to persist through even the most inconceivable challenges.

# PREFACE

The following thesis has been submitted in manuscript format following the formatting guidelines of the *Journal for Nature Conservation*.

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# CHAPTER 1

Temporal effectiveness of biodiversity surrogates in coral reefs in the British Virgin Islands

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## Abstract

Taxonomic diversity on coral reefs has declined due to anthropogenic stressors. These declines have motivated monitoring programs to estimate species richness for major taxonomic groups: fish and corals. Due to logistical challenges of species identification, there have been efforts attempting to estimate species richness on reefs using landscape features as surrogates, simple indicators that provide an estimate of a target component of biodiversity, often referred to more simply as a target. Many of these efforts are limited in spatial or temporal scope, focus on rugosity and coral cover as predictors, and use coral and fish richnesses as proxies for total species richness. Here we examine how top surrogate-target relationships vary over 27 years and across 8 study sites. We also examine whether frequently measured landscape features of reefs can serve as reliable surrogates for sponge richness. Finally, this study is one of the first to investigate the ability of sponge cover to predict richness of dominant taxonomic groups on coral reefs. This study provides additional support to the idea that surrogate-target relationships should be assessed over space and time because it can provide insight into these relationships and how the ecosystem changes. We also show that including sponges in monitoring studies may provide a broader understanding of how biodiversity is changing on reefs.

*Keywords:* biodiversity surrogate, British Virgin Islands, Caribbean, coral diversity, fish diversity, sponge diversity.

## Introduction

Biodiversity declines associated with increasing levels of anthropogenic impact are of great concern because they reflect loss of species, disruption of community dynamics and diminished ecosystem function (Dobson et al., 2006; Duffy, 2009; Ehrlich & Wilson, 1991; Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994; Staudinger et al., 2013; Stork, 2010). Documenting these declines is based on tracking different aspects of biodiversity (i.e. landscape, ecosystem, taxonomic, and genetic) over time and space (Duelli & Obrist, 2003; Noss, 1990). Taxonomic diversity, particularly species richness (a count of species in a defined area), is the most commonly studied component of biodiversity in ecological and conservation-related field research because it offers a simple, intuitive measure of biodiversity that can be readily compared across similar environments (Blake & Loiselle, 2000; Rahbek & Graves, 2001).

Monitoring species richness requires substantial taxonomic expertise (Derraik et al., 2002; Hirst, 2008; Sebek et al., 2012). Even for taxonomic groups that can be completely inventoried in principle, monitoring strategies that could detect all species in a given habitat are often prohibitively expensive and time-consuming (Kati et al., 2004). Because a complete inventory of species present in an area is unattainable in many ecosystems, particularly in high diversity systems, surrogates are often used their place. Surrogates are simple indicators that provide an estimate of a target component of biodiversity, often referred to more simply as a target (Noss, 1990).

Several types of biological and abiotic surrogate have been developed as indicators of species richness targets. Biological surrogates can be classified as “higher-taxa surrogates”, when a taxon at a higher level is used as a surrogate for the species richness of taxa at lower taxonomic levels, “cross-taxa surrogates”, when species richness of one taxon is used as a surrogate for species richness of another taxon at the same taxonomic level, or “subset-taxa surrogates” when one taxon acts as a surrogate for a larger target group of which it is a part (Mellin et al., 2011). Abiotic surrogates include variables related to resource use (e.g. light, nutrients), variables influencing physiological tolerances (e.g. temperature), and variables indirectly related to either of these (e.g. depth, latitude; McArthur et al., 2010).

An effective surrogate has two essential features: first, it takes less time, money, and experience to measure than the target and second, it maintains a consistently strong correlation with the target over space and time (Colwell & Coddington, 1994; Magierowski & Johnson, 2006; Moreno, Rojas, Pineda, & Escobar, 2007). Several studies have evaluated how effectively surrogates predict patterns of species richness across sites (Anderson, Diebel, Blom, & Landers, 2005; Darling et al., 2017; Eglington, Noble, & Fuller, 2012; Smale, 2010). The prevalence of studies analyzing the spatial predictability of surrogates may be due to their widespread use to identify priority conservation areas; this task requires an understanding of how the size and dispersion of the areas being conserved affects the relationship between the surrogate and the target (Margules, Pressey, & Williams, 2002; Padoa-Schioppa, Baietto, Massa, & Bottoni, 2006; T. J. Ward, Vanderklift, Nicholls, & Kenchington, 1999). However, few studies have explicitly investigated surrogate effectiveness over time, and those that have are typically quite short (e.g., 13 months and 1 year; Magierowski & Johnson, 2006; Rubal, Veiga, Vieira, & Sousa-Pinto, 2011). Although not well-studied, several authors have argued that an effective surrogate must maintain a stable relationship with the target over time, in other words any environmental changes that influence the target must have a qualitatively similar influence on the surrogate (Bevilacqua, Mistri, Terlizzi, & Munari, 2018; Lewandowski, Noss, & Parsons, 2010; Mellin et al., 2011).

Our main aim was thus to study how surrogate-target relationships vary in space and time, with a particular emphasis on multi-decadal temporal changes. We used coral reefs as a study system because they support high biodiversity and have been strongly affected globally over the past several decades by natural and anthropogenic stressors, including storms, ocean acidification, persistent high temperatures, coastal development, and overfishing (Comeau, Lantz, Edmunds, & Carpenter, 2016; Hughes, 1994; Hughes et al., 2017).

As is true for most ecosystems, the monitoring of species richness on coral reefs has been biased towards a few taxonomic groups. Fishes and hard corals (Scleractinia) dominate assessments of biodiversity on coral reefs, which is understandable because these groups are of functional importance ecologically (Bellwood, Hughes, Folke, & Nyström, 2004) and economically important to humans (Gill, Schuhmann, & Oxenford, 2015; Jennings & Polunin, 1996). Concerns regarding declines in the total abundance of corals and fish have motivated research documenting the species richness of these groups in order to better understand patterns and causes of decline (Mouillot et al., 2014; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011). However, recent studies, particularly those using environmental DNA (eDNA) (Deiner et al., 2017), have highlighted the presence of many other taxa on coral reefs that are typically small or cryptic, whose presence has not been well-documented, but can contribute considerably to overall species-richness (Pearman et al., 2018; Stat et al., 2017).

Because corals and fish are such conspicuous, well-studied taxonomic groups, they have been used as cross-taxa surrogates (their species richness is extrapolated to represent the richness of other coral reef taxa) or subset-taxa surrogates (their richness is extrapolated to represent total species richness) (Graham et al., 2006). The reliability of these extrapolations is not well-studied, and we used sponges as a case study in order to assess whether surrogates for fish and coral species richness can be used to predict the richness of other groups. We selected sponges because they represent a common benthic group that is of functional importance (Bell, 2008), yet relatively few studies have investigated temporal patterns in their abundance or species richness (Berman et al., 2013; Wulff, 2006).

Researchers have used a variety of criteria when selecting surrogates (Noss, 1990). We selected two simple biotic surrogates (total coral cover and total sponge cover) and one abiotic surrogate (reef rugosity) for largely practical reasons. Total coral cover (the proportion of reef surface covered by live Scleractinian coral) is the simplest potential higher-taxa surrogate for coral species richness and is arguably the most widely-monitored variable in this ecosystem (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Gardner, Côté, Gill, Grant, & Watkinson, 2003; Jackson, Donovan, Cramer, & Lam, 2014). Reef rugosity (a simple measure of surface roughness) has also been monitored routinely by coral reef biologists and is expected to be a good abiotic surrogate for fish species richness because the habitat requirements of many fishes include structural reef features. Higher rugosity should thus provide structure that may be utilized by a greater number of fish species (Darling et al., 2017; Graham et al., 2006; Gratwicke & Speight, 2005; Newman et al., 2015). Rugosity is also potentially a better surrogate for fish species richness than live coral cover because, even though corals create structure, many fish species utilize structural reef features even when the coral is dead (Wilson, Graham, Pratchett, Jones, & Polunin, 2006). Although less-widely monitored than coral cover or rugosity, we also selected sponge cover (the proportion of reef surface covered by live sponges) as the simplest potential higher-taxa surrogate for sponge species richness.

Our goal was to understand whether monitoring of cost-effective surrogates is appropriate in tracking changes in the species richness of coral reef communities. We specifically tested how surrogate-target relationships vary over time and space using 27 years of monitoring data from eight sites around Guana Island in the British Virgin Islands (Forrester et al., 2015). Our first objective was to determine which of our three candidate surrogates (coral cover, sponge cover, rugosity) was most strongly correlated with each of four separate targets (species richness of corals, fishes, sponges, and richness of the three groups pooled). Our second objective was to determine if the relationships between the surrogate and corresponding target remain consistent among sites and, most importantly, over time.

## Material and Methods

### Field study design

We used data collected as part of an ongoing monitoring program at eight sites around Guana Island in the British Virgin Islands (Forrester et al., 2015; Fig. 1). All sites were similar in covering 0.6-1.0 hectares of sloping fringing coral reef adjacent to the island at a depth of 9-10 m. Sites varied in exposure to prevailing weather; sites on the windward north side of the island are more exposed to prevailing winds and swell than those on the southern leeward side (Fig. 1). Although distributed across a gradient of prevailing wave exposure, the sites were similar enough in other respects that they represent broadly similar habitats. In other words, we assume that spatio-temporal shifts in species richness primarily reflect changes in α (local) diversity, rather than differences between habitats (β-diversity) (Whittaker, 1960). Corals, fishes, and rugosity were sampled annually between June and August from 1992-2018. Logistical constraints meant that sponges were not sampled in all years (no counts in 1992, 1996-1999, 2004, 1993 at Crab Cove, 2014 at Pelican Ghut, and 2017 at Bigelow Beach and Pelican Ghut). All surveys were performed using 30-m transects, placed at haphazardly selected locations within each site. The number of transects sampled per site varied among years (n = 3-22). However, because species-richness estimates are dependent on sampling effort, we opted to standardize to three transects per site per year. The three transects for analysis were selected at random.

### Survey methods

Corals, sponges, fishes, and rugosity were sampled using well-established visual survey methods. Surveys were conducted with the approval of the BVI Department of Conservation and Fisheries, and fish counts were approved by the URI Institutional Animal Care and Use Committee (protocol AN13-04-016). Fishes were counted within a belt transect 30 m long x 1.5 m wide, and a T-shaped bar was used to determine the transect width as the diver swam along the transect line. Fish counts were restricted to species that are amenable to visual survey; that is, day-active species that are relatively site-attached and reliably visible to divers (Willis, 2001). Nocturnal species, highly mobile groups such as mackerels (Scombridae) and jacks (Carangidae) that are transient visitors to the sites, and small cryptic groups like gobies (Gobiidae) and blennies (Blennioidei) that often hide in crevices were not surveyed. Newly recruited juvenile fishes (< 1 month on the reef) were also excluded because their abundance is affected by lunar cycles, which complicates the detection of long-term trends (Robertson, 1992). Because fish were the only mobile organisms surveyed, the fish survey was conducted first for each transect in order to reduce any bias caused by divers disturbing the fish (Emslie, Cheal, MacNeil, Miller, & Sweatman, 2018).

Corals were surveyed using the linear point-intercept method, wherein a diver swam along the tape and identified the taxon under the tape at 0.25 m intervals (n = 120 points per transect; Canfield, 1941). Corals encountered were identified to species, where possible, and other taxa encountered (including sponges) were classified into broader groupings. The point-intercept data was thus used to estimate coral species richness as well as the total abundance (% cover) of hard corals and total % cover of sponges (Almada-Villela, Sale, Gold-Bouchot, & Kjerfve, 2003). Because % cover of sponges was generally lower than that of corals, we used a different method to estimate sponge richness that was designed to sample a greater number of sponge colonies along each transect. To estimate sponge species richness, sponges were surveyed using a line intercept method in which any sponge that intercepted the transect was recorded and identified to species, where possible.

Rugosity was measured as a proxy for three-dimensional structural complexity using the consecutive height difference method (McCormick, 1994), where a diver records the difference between the height of the transect tape and the substrate at 1 m intervals along the first 10 m of each transect. Rugosity (in cm) is calculated as the square root of the sum of the squared differences between successive height measurements. A rugosity value of 0 is flat and vertical complexity increases as the rugosity value increases.

Because identifying taxa to species is not always possible or practical in field surveys, fish, corals, and sponges were identified to the most specific taxonomic group possible (Tables A.1-A.2). All fish were identified to species, while corals and sponges were sometimes identified as multi-species recognizable taxonomic units (D. F. Ward & Stanley, 2004), or RTU’s, for the following reasons: (1) taxonomists reassigned taxa thought to be different species to the same species after the study began, (2) taxonomists divided a single species into multiple species after the study began, and (3) several species are visually indistinguishable in the field. In all cases, the lowest resolution RTU was used, and for simplicity RTU’s are referred to as “species” hereafter.

To minimize bias introduced by using multiple observers, fish counts and sponge counts were each made by a single expert observer (Bernard, Götz, Kerwath, & Wilke, 2013; Thompson & Mapstone, 1997). Both observers, however, compared their counts to those of another fish and sponge expert respectively. These observers independently surveyed the same transects as the authors during one year and their species identifications were consistent with the authors’ (data not shown). Coral data were collected by three observers, but new observers’ species identifications and counts were calibrated with those of another observer during a training period of at least 15 dives before their data were incorporated into the study.

### Statistical Analysis

We used sites as replicates because they represent spatial units large enough to be analogous to areas monitored to assess local conservation and management actions. For surrogates (coral cover, sponge cover, and rugosity), replicates were thus means for the 3 randomly-selected transects per site per year. To estimate species richness, we pooled the 3 randomly-selected transects for each year and site and calculated the total number of species observed. Richness was calculated separately for each of the three focal taxonomic groups (fish, corals, and sponges), and combined species richness was thus only calculated for sites and years for which richness of all three taxonomic groups was available.

Species richness is a count variable that takes non-negative integer values and is prone to overdispersion. We therefore used negative binomial regression using the ‘MASS’ package in the R statistical programming language (R Core Team, 2019) to model species richness (Venables & Ripley, 2002). All models include the parameter, theta (θ), which accounts for overdispersion. Graphical assessment revealed no patterns in the Pearson residuals or deviance residuals for any of the models included in the analysis, indicating the data conformed to the assumptions of the negative binomial models used.

To determine which of the candidate surrogates was most strongly associated with each of the targets, we used simple models with only the candidate surrogates as predictors. We then compared these simple, surrogate-only models using Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). AICc results provide a measure of parsimony in that they can be used to identify models with the fewest parameters and the greatest explanatory ability relative to other models in the model set. We considered the most supported models to be those within 2 AICc units of the most parsimonious model. Pseudo-r-squared values were also used for model interpretation by providing a measure of goodness-of-fit in that they can be used to compare how much each surrogate improves the ability to predict a given target. Pseudo-r-squared values were used in place of traditional r-squared values because the negative binomial distribution uses a log link function, for which there is no equivalent statistic to traditional r-squared as a measure of goodness-of-fit. We used Nagelkerke’s pseudo-r-squared (*R*N2) instead of other pseudo-r-squared metrics because it scales like traditional r-squared (ranges from 0-1) and is used to evaluate the improvement from a null to a fitted model. Only the top surrogate identified for each target from this comparison was used for subsequent modeling.

We also examined simple correlations between the targets (between coral, fish, and sponge richnesses), as well as between the surrogates (between percent hard coral cover, rugosity, and percent sponge cover), to inform interpretations of the models.

To determine if relationships between top surrogates and the targets remain consistent over space and time, we added additional terms to the surrogate-only models to account for temporal variation and variation across sites. Site is a categorical predictor of the 8 locations around Guana Island and year models year-to-year trends over the duration of the study (27 years). For each of the targets (dependent variables), AICc was used to compare surrogate-only models to models with additional terms for year, site, and year plus site to test for variation in the data over time, across sites, or over time and across sites that cannot be accounted for by the surrogate alone. These additive models were also compared to models with interactive terms for the surrogate with year and the surrogate with site. These interactive models would suggest that the relationship between the target and the top candidate surrogate changes over time or across sites. We did not consider more complex models with higher-order interaction terms for this study because, if more complex models were supported, the relationship between the candidate surrogate and the target would not be valuable for monitoring purposes. In other words, the ecological interpretation of these more complex models would be complicated enough that there would be no clear relationship between the candidate surrogate and the target, suggesting that the candidate surrogates do not provide the benefits of a good surrogate. We used the same model selection procedure as above, where top models were those with delta AICc ≤ 2 and AICc weights > 50%. Nagelkerke’s pseudo-r-squared values (*R*N2) were also used for additional model support.

All data management and analysis was performed in version 3. 5. 3 of the R programming language (R Core Team, 2019).

## Results

### Summary statistics

We recorded 205 species across all 27 years for all 8 sites around Guana Island. There were 117 fish species, 30 coral species, and 58 sponge species. For each site and year combination, coral richness ranged from 4 to 22 (mean = 13; standard deviation = 4), sponge richness ranged from 8 to 36 (mean = 22; standard deviation = 5), fish richness ranged from 9 to 37 (mean = 24; standard deviation = 6), and combined richness ranged from 39 to 75 (mean = 59; standard deviation = 8). Percent coral cover ranged from 2.68 to 61.75 (mean = 21.36; standard deviation = 13.95), percent sponge cover ranged from 0.28 to 27.77 (mean = 7.96; standard deviation = 4.98), and rugosity (in cm) ranged from 17 to 78 (mean = 45; standard deviation = 16).

### Basic associations

Fish richness and coral richness were positively correlated, whereas sponge richness was negatively correlated to both of these, suggesting sponge richness varied in space and time independent of changes in fish and coral richness (Fig. A.3). Similarly, rugosity and coral cover were positively correlated, whereas sponge cover was weakly and negatively correlated to both of these, suggesting sponge cover also varied in space and time independent of changes in rugosity and coral cover (Fig. A.4).

### Objective 1: Identify top candidate surrogates

Coral cover and rugosity were both positively correlated with coral richness, but the correlation was stronger for coral cover and so it was the top candidate surrogate for coral richness (Table 1; Fig. 2). Sponge cover showed a weak positive association with sponge richness, and there was a weak negative association between coral cover and sponge richness. Coral cover, however, was a slightly better predictor of sponge richness than sponge cover and so, although none of the surrogates were highly correlated with the target, coral cover was the top candidate surrogate (Table 2; Fig. 2). Fish species richness was positively correlated with both coral cover and rugosity, but rugosity was the best predictor of fish richness and was the top candidate surrogate for fish richness (Table 3; Fig. 2) and combined richness (Table 4; Fig. 2).

### Objective 2: Top candidate surrogates over time and space

#### Coral Richness:

Variation in coral richness can partially be explained by coral cover as a candidate surrogate. However, the model with coral cover and year was the most competitive (*R*N2 = 0.69; Table 5), which means there were changes in coral richness over time that were not explained by the candidate surrogate alone. This suggests that there were temporal events that affected coral richness and coral cover differently. Evidence to support this can be seen by looking at each of these variables over time; average coral richness increased slightly over the study period, whereas coral cover steadily declined throughout the same period (Fig. A.5). There was also support that the nature of the relationship between coral cover and coral richness (i.e. the slope of the relationship) changed over time (Table 5). In other words, the surrogate-target relationship was not stable over time because coral species richness increased over time for a given amount of coral cover. For example, a reef with 20 percent coral cover in 1992 was predicted to have about 9 coral species, whereas in 2018 it was predicted to have about 17 coral species (Fig. 3).

#### Sponge Richness:

Coral cover was the best predictor of sponge richness of the three candidate surrogates, but sponge richness was not well-predicted by any of our candidate surrogates (Fig. 2). There was thus considerable unexplained variation in sponge richness, some of which was associated with differences among sites and with change over time (*R*N2 = 0.71; Table 6). Unexplained spatial differences among the 8 sites had a greater influence on sponge richness than they did on coral cover (Fig. 4). For a given site, predicted sponge richness varied by about 2-3 species across the observed gradient of coral cover. Whereas, for a given amount of coral cover, predicted sponge richness differed by up to 8-9 species. With regards to temporal variation, sponge species richness slightly increased over the monitoring period for a given amount of coral cover. A site was likely to have about 3 more sponge species at the end of the monitoring period than at the beginning (Fig. 5). In summary, the surrogate-target relationship for sponge richness was weak and unstable in both space and time.

#### Fish Richness:

Fish richness can partially be explained by rugosity as a candidate surrogate. However, the top model had terms for both rugosity and site (*R*N2 = 0.82; Table 7), suggesting there were variations in fish richness across sites that were not explained by rugosity alone. These spatial variations among the 8 sites were likely due to the fact that, apart from White Bay (change in rugosity from 19-60 cm) and Crab Cove (change in rugosity from 26-57 cm), the other 6 sites remained quite distinct in rugosity over time. For example, Pelican Ghut had the lowest rugosity throughout the monitoring period, and correspondingly low fish richness (Fig. 6). Monkey Point had the next lowest rugosity and the next lowest fish richness, and so on. This may explain why the site-specific regression lines (Fig. 6) have shallower slopes than a line fit through all of the data (Fig. 2). In summary, the relationship between rugosity and fish richness was consistent over time, and, because rugosity varied more across sites than within a site, fish richness remained relatively stable over site and time and can be estimated by rugosity. Given this, sites with similar values for rugosity should have similar values of fish richness and this is evidence that rugosity can serve as an effective surrogate for fish richness.

#### Combined Richness:

Combined richness can partially be explained by rugosity as a candidate surrogate. However, the top model had terms for rugosity, year, and site (*R*N2 = 0.65; Table 8), suggesting there were variations in combined richness across sites and years that were not explained by rugosity alone. Similar to the relationship between rugosity and fish richness, these spatial variations among the 8 sites were likely due to distinct rugosity values for each site over time. The sites were organized differently on the y-axis for combined richness than they were for fish richness likely driven by variations in sponge richness across sites that follow a different pattern over time (Fig. 7). Similar to the association with fish richness above, the site-specific regression lines had shallower slopes than a line fit through all of the data due to the variation in rugosity over time at White Bay and Crab Cove (Fig. 2). With regards to temporal variation, combined species richness gradually increased over the monitoring period for a given amount of rugosity; a site was likely to have about 15 more species in 2018 than it had in 1993 (Fig. 8).

In summary, rugosity varied significantly across sites and not much within a site and combined richness increased gradually over time, suggesting combined richness can be predicted by rugosity at a given site and that this combined richness is expected to increase over time for a given level of rugosity. Rugosity may serve as a surrogate for combined richness across sites, but it failed to explain the increase in combined richness over time. There may be some other ecological explanation for this, such as the increase in sponge species over time having more of an impact on combined richness than the more subtle changes in fish and coral richness over the same time period.

## Discussion

### New limitations section

We suggest that the use of RTU’s, although it affects estimates of absolute species richness, should not alter the outcome of the analysis.

### Assessing surrogate effectiveness over space and time

Local richness can vary for a variety of reasons, including: dispersal limitation, changes in environmental or landscape features, and competition over space.

Dispersal ability of reef species may be able to explain spatial variations in richness. It has been established that there is high variability in the distances traveled and dispersal mechanisms employed by different coral reef species (Jones et al., 2009). These differences in dispersal ability relate to genetic connectivity and, as a result, the biodiversity of reefs (Almany et al., 2009).

Changes in environmental or landscape features like those investigated in our study, such as rugosity and coral cover, may also be used to predict richness of taxonomic groups on coral reefs. Other studies have found that reduced coral richness resulted in a reduction of rugosity which, in turn, led to a decrease in fish abundance (Alvarez-Filip, Dulvy, Côté, Watkinson, & Gill, 2011). Although we did not include fish abundance as a target in our results, we did observe a reduction in the number of fish species and overall species present at lower levels of rugosity. We also found rugosity to be negatively associated with coral richness; however, we found coral cover to be a better surrogate of coral richness. The relationship between coral richness and coral cover varied over time; one explanation being, the increase in coral species richness for a given amount of coral cover over time is due to an increase in evenness over time. In other words, the abundance of the most dominant species is reduced over time. The study mentioned above found the variance in rugosity observed at higher levels of coral cover was the result of dominance by a particular genus of coral; some dominant corals were more structurally complex than other dominant corals (Alvarez-Filip et al., 2011). Spatial differences in rugosity governed patterns in fish richness and combined richness, and combined richness also increased over time. White Bay and Crab Cove had high variability in rugosity over time compared to other sites, suggesting there might be some factor affecting rugosity at these two sites leading to subsequent fluctuations in fish richness and combined richness.

Competition over space has been shown to be related to chemical inhibition, or allelopathy, in interspecific relationships between sponges and corals. These relationships may explain why coral cover was the top candidate surrogate for sponge richness and also why sponge cover and sponge richness are negatively correlated with coral cover and coral richness respectively. Allelopathic sponges, may reduce coral cover at local scales (Pawlik, Steindler, Henkel, Beer, & Ilan, 2007). Other studies have shown that unpalatable sponges, those that use chemicals to deter predation by fish, are also allelopathic toward corals and are relatively common on Caribbean coral reefs (Loh, McMurray, Henkel, Vicente, & Pawlik, 2015). Despite some potential benefits sponges can have on coral structures and reef nutrient cycles, even palatable sponges can outcompete corals for space by overgrowing coral structures (Loh & Pawlik, 2014; Stella, Pratchett, Hutchings, & Jones, 2011). Over time, the abundance of these palatable sponges has increased with the reduced abundance of spongivorous fish due to overfishing (Loh & Pawlik, 2014; Powell et al., 2014).

Species richness can vary across spatial and temporal scales for many reasons, some of which are described here. As such, studies proposing surrogates to predict species richness and other diversity measures should explicitly address the spatial and temporal limitations of using the candidate surrogates, especially when planning large-scale or long-term studies.

### Value of sponge monitoring

Different taxonomic groups respond differently to changes in the environment. As such, using diversity measures for one group as proxies for total biodiversity without evaluating this relationship (taxonomic surrogacy) can lead to false conclusions regarding taxonomic groups not directly measured. For example, windward reefs had higher coral and fish diversity than leeward reefs, but the latter supported higher sponge diversity (Acosta, Barnes, & McClatchey, 2015). Had this environmental gradient been extrapolated to diversity of taxonomic groups other than fish and corals, it may have been used to make management decisions that would negatively affect sponge diversity. Similarly, we found that sponges do not conform to the same patterns (over space, time, or with landscape features) as corals and fish. The traditional measures of coral cover and rugosity might be good predictors of coral richness and fish richness respectively, but caution should be exercised when making extrapolations to total reef diversity as richness of some groups, here we looked at sponge richness, is not strongly correlated with these variables. In addition, we found that sponge cover does not follow the same patterns as coral cover or rugosity over time or across sites. Perhaps sponges are not the only taxonomic group of organisms on coral reefs that are difficult to predict with coral cover or rugosity; there are many coral-associated invertebrates that may provide insight into coral reef diversity (Stella et al., 2011) and it is unlikely that all of these taxonomic groups will be adequately predicted by rugosity or coral cover alone.

Because sponge richness and sponge cover follow different patterns than other variables in this study, comparing patterns in sponges to other taxonomic groups and landscape features can provide a fuller picture of reef biodiversity. It has already been suggested that “non-umbrella” species can provide insight into overall site biodiversity at local scales in terrestrial ecosystems (Gerlach, Samways, & Pryke, 2013). As we show here, understudied taxonomic groups may not share surrogates with well-studied groups and the direction of the relationships may even be contradictory; something that has also been demonstrated in similar studies conducted in tropical forests (Lam et al., 2014). Therefore, diversity of these understudied taxonomic groups should be measured directly until a reliable surrogate can be identified. If not, studies that comment on species diversity should be transparent about which taxonomic groups they include in their estimates.

In conclusion, we show here that the commonly measured surrogates, rugosity and percent coral cover, can be reliable predictors of fish richness and coral richness respectively. However, we suggest that future reef biodiversity studies incorporate sponge-related measures to get a broader interpretation of reef biodiversity as they reveal different patterns than other measures. Reef biodiversity studies that do not incorporate sponge-related measures should be explicit about the taxonomic groups included in the analyses and exercise caution when estimating total reef biodiversity.

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## Tables

Table 1. AICc table of models with coral richness as the response variable (target) and the candidate surrogates as predictors. The intercept model represents the null with no surrogates. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| coralcover | 3 | 1058.2 | 0.0 | 1.00 | -526.1 | 0.62 |
| rugosity | 3 | 1131.2 | 73.0 | 0.00 | -562.5 | 0.23 |
| spongecover | 3 | 1161.1 | 102.8 | 0.00 | -577.5 | 0.03 |
| intercept | 2 | 1163.5 | 105.3 | 0.00 | -579.7 | NA |

Table 2. AICc table of models with sponge richness as the response variable (target) and the candidate surrogates as predictors. The intercept model represents the null with no surrogates. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| coralcover | 3 | 967.5 | 0.0 | 0.96 | -480.7 | 0.28 |
| spongecover | 3 | 973.9 | 6.4 | 0.04 | -483.9 | 0.24 |
| rugosity | 3 | 995.4 | 27.9 | 0.00 | -494.6 | 0.05 |
| intercept | 2 | 999.0 | 31.5 | 0.00 | -497.5 | NA |

Table 3. AICc table of models with fish richness as the response variable (target) and the candidate surrogates as predictors. The intercept model represents the null with no surrogates. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| rugosity | 3 | 1266.3 | 0.0 | 1.00 | -630.1 | 0.63 |
| coralcover | 3 | 1295.4 | 29.2 | 0.00 | -644.7 | 0.53 |
| spongecover | 3 | 1359.7 | 93.4 | 0.00 | -676.8 | 0.21 |
| intercept | 2 | 1389.9 | 123.6 | 0.00 | -692.9 | NA |

Table 4. AICc table of models with combined richness, as the sum of coral, fish, and sponge richness, as the response variable (target) and the candidate surrogates as predictors. The intercept model represents the null with no surrogates. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| rugosity | 3 | 1106.8 | 0.0 | 0.99 | -550.3 | 0.38 |
| coralcover | 3 | 1116.3 | 9.6 | 0.01 | -555.1 | 0.32 |
| intercept | 2 | 1152.6 | 45.9 | 0.00 | -574.3 | NA |
| spongecover | 3 | 1153.8 | 47.1 | 0.00 | -573.8 | 0.01 |

Table 5. AICc table of models with coral richness as the response variable (target) and percent coral cover as the top candidate surrogate. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| coralcover + year | 4 | 1044.2 | 0.0 | 0.58 | -518.0 | 0.69 |
| coralcover + year + year\*coralcover | 5 | 1045.6 | 1.4 | 0.29 | -517.7 | 0.69 |
| coralcover + year + site | 11 | 1047.2 | 2.9 | 0.13 | -511.9 | 0.74 |
| coralcover | 3 | 1058.2 | 14.0 | 0.00 | -526.1 | 0.62 |
| coralcover + site | 10 | 1062.5 | 18.3 | 0.00 | -520.7 | 0.67 |
| coralcover + site + site\*coralcover | 17 | 1064.2 | 19.9 | 0.00 | -513.5 | 0.72 |

Table 6. AICc table of models with sponge richness as the response variable (target) and percent coral cover as the top candidate surrogate. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| coralcover + year + site | 11 | 909.3 | 0.0 | 1.00 | -442.8 | 0.71 |
| coralcover + site | 10 | 922.3 | 12.9 | 0.00 | -450.4 | 0.64 |
| coralcover + site + site\*coralcover | 17 | 933.8 | 24.5 | 0.00 | -447.8 | 0.67 |
| coralcover + year | 4 | 966.3 | 56.9 | 0.00 | -479.0 | 0.31 |
| coralcover + year + year\*coralcover | 5 | 966.6 | 57.3 | 0.00 | -478.1 | 0.32 |
| coralcover | 3 | 967.5 | 58.2 | 0.00 | -480.7 | 0.28 |

Table 7. AICc table of models with fish richness as the response variable (target) and rugosity (in cm) as the top candidate surrogate. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| rugosity + site | 10 | 1203.8 | 0.0 | 0.75 | -591.4 | 0.82 |
| rugosity + year + site | 11 | 1206.0 | 2.2 | 0.25 | -591.4 | 0.82 |
| rugosity + site + site\*rugosity | 17 | 1217.0 | 13.2 | 0.00 | -590.0 | 0.83 |
| rugosity + year + year\*rugosity | 5 | 1260.9 | 57.1 | 0.00 | -625.3 | 0.65 |
| rugosity + year | 4 | 1261.6 | 57.8 | 0.00 | -626.7 | 0.65 |
| rugosity | 3 | 1266.3 | 62.4 | 0.00 | -630.1 | 0.63 |

Table 8. AICc table of models with combined richness, as the sum of coral, fish, and sponge richness, as the response variable (target) and rugosity (in cm) as the top candidate surrogate. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and *R*N2 isNagelkerke’s pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model Name** | **K** | **AICc** | **Delta AICc** | **Akaike weight** | **Log-likelihood** | ***R*N2** |
| rugosity + year + site | 11 | 1079.7 | 0.0 | 0.96 | -528.0 | 0.65 |
| rugosity + site | 10 | 1086.5 | 6.8 | 0.03 | -532.5 | 0.60 |
| rugosity + year | 4 | 1092.8 | 13.1 | 0.00 | -542.3 | 0.49 |
| rugosity + site + site\*rugosity | 17 | 1093.2 | 13.5 | 0.00 | -527.5 | 0.65 |
| rugosity + year + year\*rugosity | 5 | 1094.8 | 15.1 | 0.00 | -542.2 | 0.49 |
| rugosity | 3 | 1106.8 | 27.0 | 0.00 | -550.3 | 0.38 |

## Figures



Figure 1. Top panel: a map of Guana Island, British Virgin Islands showing the eight study sites: (1) Grand Ghut, (2) Pelican Ghut, (3) Bigelow Beach, (4) Monkey Point, (5) White Bay, (6) Iguana Head, (7) Crab Cove, and (8) Long Point, also known as Muskmelon. Lower panel: the location of Guana Island within the British Virgin Islands.

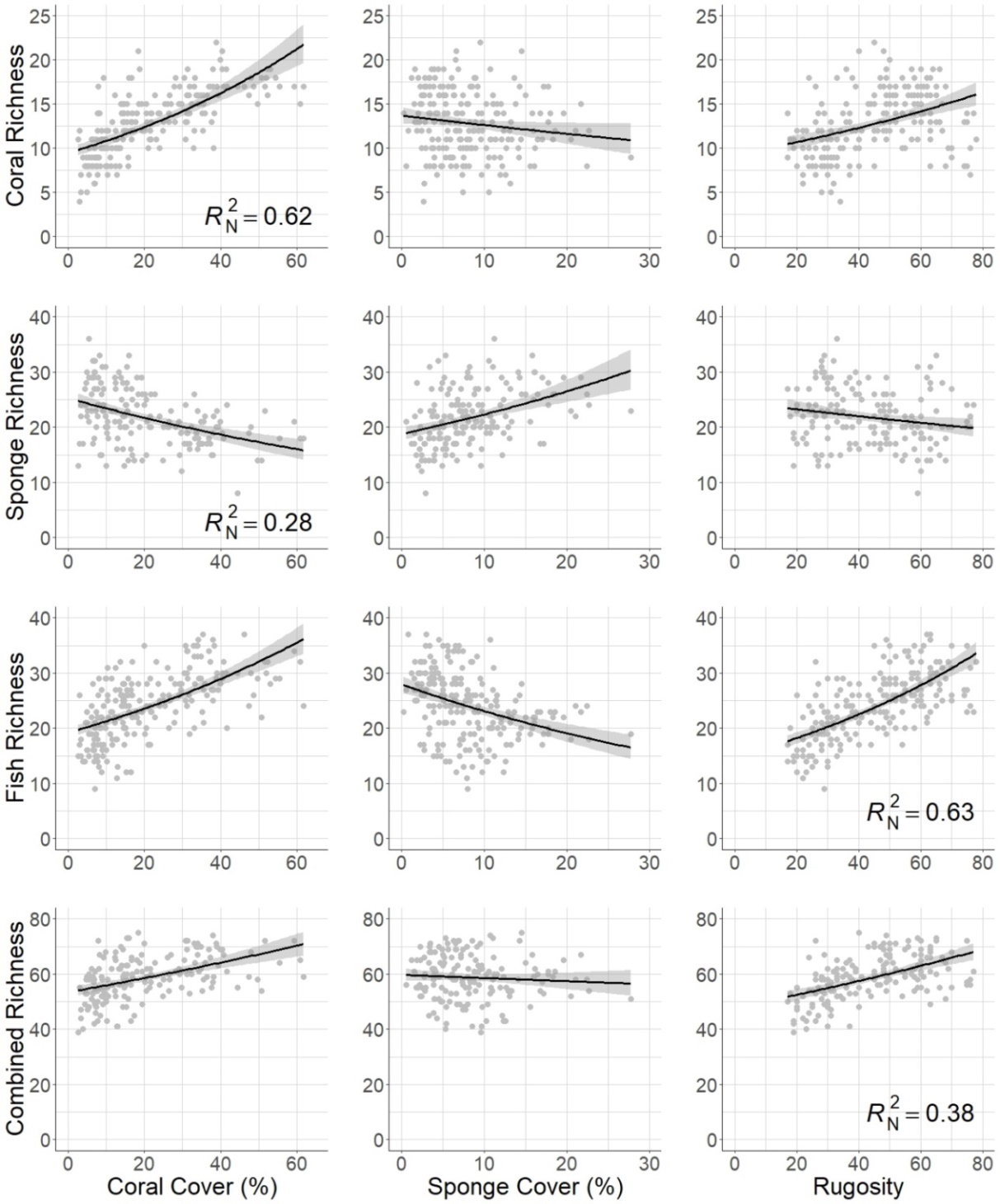


Figure 2. Lines represent smoothed conditional means using the negative binomial distribution and the formula y ~ x, where y is a target (rows) and x is a surrogate (columns). Shaded portions represent 95% confidence intervals of fitted values. Nagelkerke’s pseudo-r-squared values (*R*N2) are shown for the top (i.e. most competitive) surrogate for each target. Rugosity measured in centimeters. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

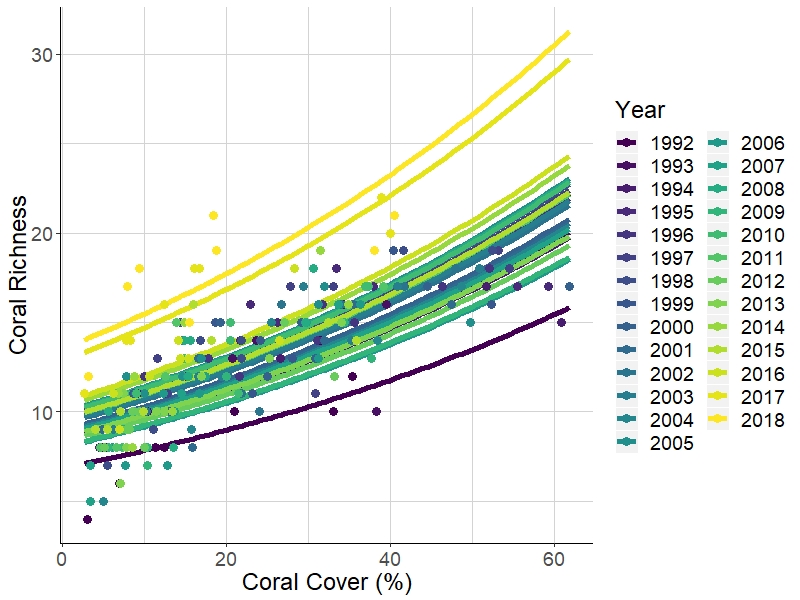


Figure 3. This figure helps to visualize changes in coral richness for a given amount of coral cover over a 27 year period. Solid lines represent predictions colored by year using the negative binomial distribution and the formula y ~ x + year, where y is coral richness, x is coral cover, and year is a categorical predictor. The formula y ~ x + year, with year as a trend, was the most competitive model to predict coral richness. Confidence intervals are not shown. Points represent observed values colored by year. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

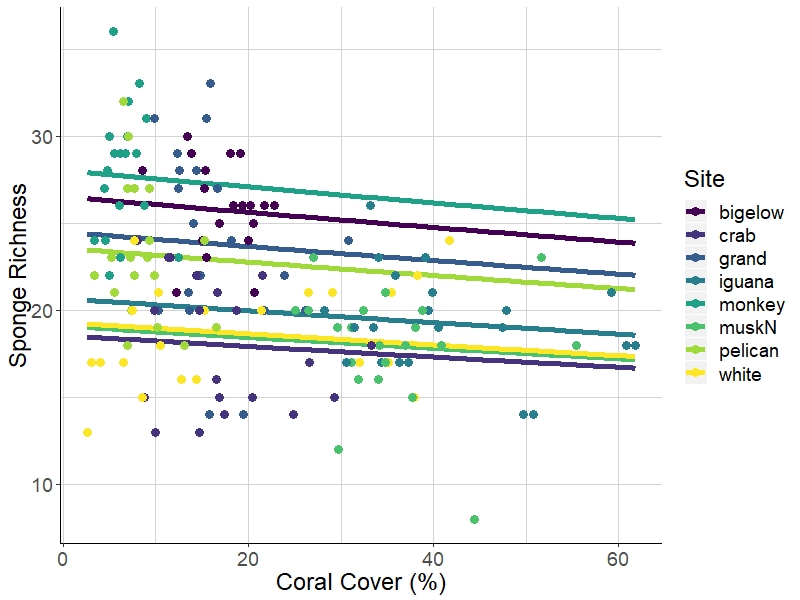


Figure 4. This figure helps to visualize differences in sponge richness for a given amount of coral cover among 8 coral reefs around Guana Island, BVI. Solid lines represent predictions colored by site using the negative binomial distribution and the formula y ~ x + site, where y is sponge richness, x is coral cover, and site is a categorical predictor. The formula y ~ x + year + site, with year as a trend, was the most competitive model to predict sponge richness. Confidence intervals are not shown. Points represent observed values colored by year. Data were collected from 1992-2018.

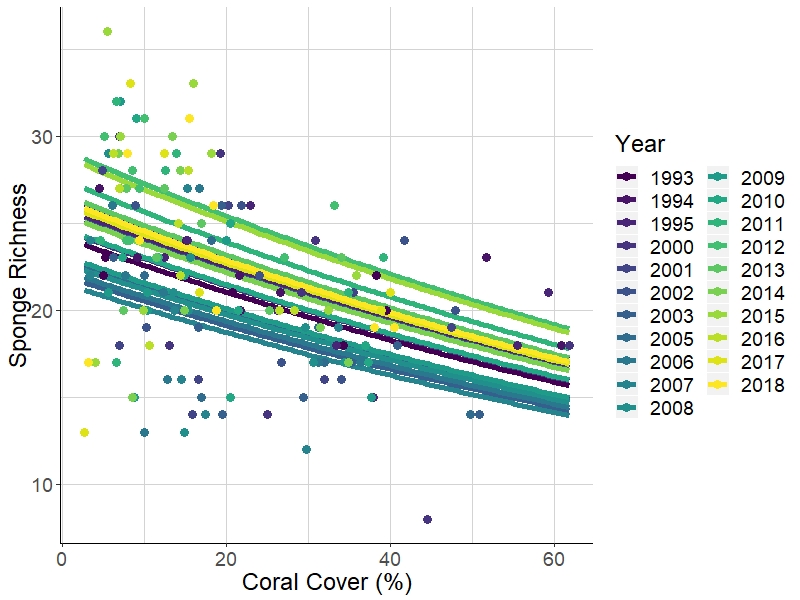


Figure 5. This figure helps to visualize changes in sponge richness for a given amount of coral cover over a 27 year period. Solid lines represent predictions colored by year using the negative binomial distribution and the formula y ~ x + year, where y is sponge richness, x is coral cover, and year is a categorical predictor. The formula y ~ x + year + site, with year as a trend, was the most competitive model to predict sponge richness. Confidence intervals are not shown. Points represent observed values colored by year. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

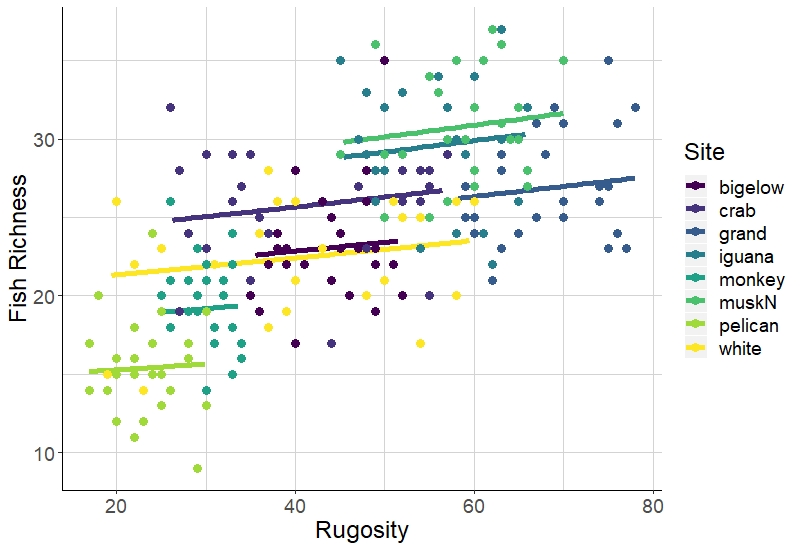


Figure 6. This figure helps to visualize differences in fish richness for a given amount of rugosity among 8 coral reefs around Guana Island, BVI. Solid lines represent predictions colored by site using the negative binomial distribution and the formula y ~ x + site, where y is fish richness, x is rugosity in cm, and site is a categorical predictor. Lines are truncated to correspond with the observed ranges of rugosity for each site. The formula y ~ x + site was the most competitive model to predict fish richness. Confidence intervals are not shown. Points represent observed values colored by year. Data were collected from 1992-2018.

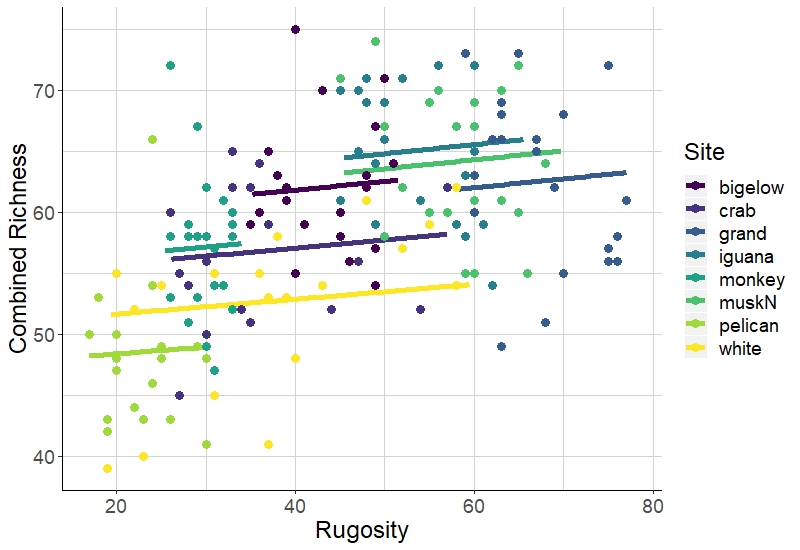


Figure 7. This figure helps to visualize differences in combined richness, as the sum of coral, fish, and sponge richness, for a given amount of rugosity among 8 coral reefs around Guana Island, BVI. Solid lines represent predictions colored by site using the negative binomial distribution and the formula y ~ x + site, where y is combined richness, x is rugosity in cm, and site is a categorical predictor. Lines are truncated to correspond with the observed ranges of rugosity for each site. The formula y ~ x + year + site, with year as a trend, was the most competitive model to predict combined richness. Confidence intervals are not shown. Points represent observed values colored by year. Data were collected from 1992-2018.

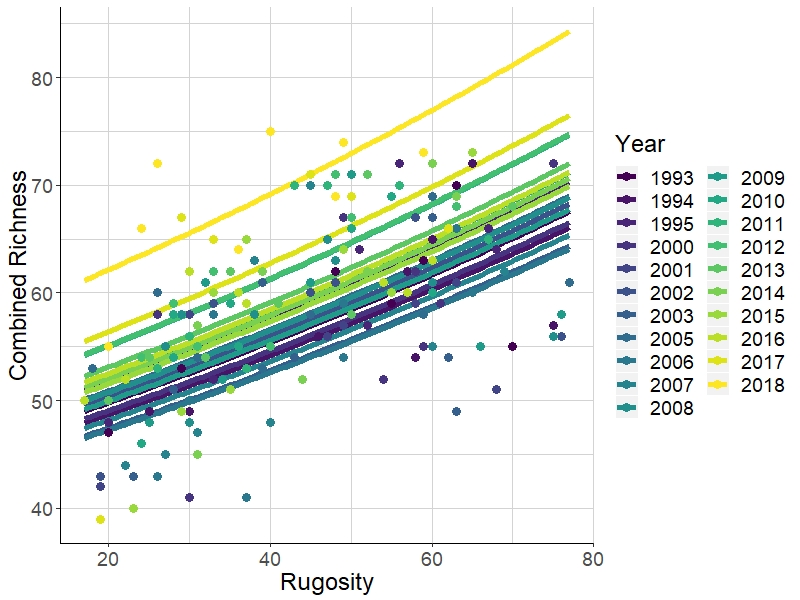


Figure 8. This figure helps to visualize changes in combined richness, as the sum of coral, fish, and sponge richness, for a given amount of rugosity over a 27 year period. Solid lines represent predictions colored by year using the negative binomial distribution and the formula y ~ x + year, where y is combined richness, x is rugosity in cm, and year is a categorical predictor. The formula y ~ x + year + site, with year as a trend, was the most competitive model to predict combined richness. Confidence intervals are not shown. Points represent observed values colored by year. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

## Appendices

Table A.1. Fish species included in richness calculations.

|  |  |  |  |
| --- | --- | --- | --- |
| Fish species | Fish common name | Fish species cont. | Fish common name cont. |
| *Abudefduf saxatilis* | Sergeant major | *Hypoplectrus chlorurus* | yellowtail hamlet |
| *Acanthurus bahianus* | ocean surgeon | *Hypoplectrus guttavarius* | shy hamlet |
| *Acanthurus chirurgus* | doctorfish | *Hypoplectrus indigo* | indigo hamlet |
| *Acanthurus coeruleus* | blue tang | *Hypoplectrus nigricans* | black hamlet |
| *Aluterus scriptus* | scrawled filefish | *Hypoplectrus puella* | barred hamlet |
| *Amblycirrhitus pinos* | redspotted hawkfish | *Hypoplectrus sp.* | tan hamlet |
| *Anisotremus surinamensis* | black margate | *Hypoplectrus unicolor* | butter hamlet |
| *Anisotremus virginicus* | porkfish | *Inermia vittata* | boga |
| *Aulostomus maculatus* | trumpetfish | *Kyphosus sectatrix* | gray chub |
| *Balistes capriscus* | gray triggerfish | *Lachnolaimus maximus* | hogfish |
| *Balistes vetula* | queen triggerfish | *Lactophrys bicaudalis* | spotted trunkfish |
| *Bodianus rufus* | Spanish hogfish | *Lactophrys quadricornis* | scrawled cowfish |
| *Calamus calamus* | saucereye porgy | *Lactophrys triqueter* | smooth trunkfish |
| *Calamus pennatula* | pluma porgy | *Lutjanus apodus* | schoolmaster snapper |
| *Cantherhines macrocerus* | whitespotted filefish | *Lutjanus griseus* | gray snapper |
| *Cantherhines pullus* | orangespotted filefish | *Lutjanus jocu* | dog snapper |
| *Canthigaster rostrata* | sharp-nose puffer fish | *Lutjanus mahogoni* | mahogany snapper |
| *Centropyge argi* | cherubfish | *Lutjanus synagris* | lane snapper |
| *Chaetodipterus faber* | Atlantic spadefish | *Melichthys niger* | black durgon |
| *Chaetodon ocellatus* | spotfin butterflyfish | *Microspathodon chrysurus* | yellowtail damselfish |
| *Chaetodon sedentarius* | reef butterflyfish | *Monacanthus ciliatus* | fringed filefish |
| *Chaetodon striatus* | banded butterflyfish | *Monacanthus tuckeri* | slender filefish |
| *Chaetodon capistratus* | foureye butterflyfish | *Mulloidichthys martinicus* | yellow goatfish |
| *Chromis cyanea* | blue chromis | *Mycteroperca tigris* | tiger grouper |
| *Chromis insolata* | sunshinefish | *Mycteroperca venenosa* | yellowfin grouper |
| *Chromis multilineata* | brown chromis | *Nicholsina usta* | emerald parrotfish |
| *Clepticus parrae* | creole wrasse | *Ocyurus chrysurus* | yellowtail snapper |
| *Cryptotomus roseus* | bluelip parrotfish | *Odontoscion dentex* | reef croaker |
| *Diodon hystrix* | porcupinefish | *Pomacanthus arcuatus* | gray angelfish |
| *Epinephelus adscensionis* | rock hind | *Pomacanthus paru* | French angelfish |
| *Epinephelus guttatus* | red hind | *Pomacentrus diencaeus* | longfin damselfish |
| *Epinephelus cruentatus* | graysby | *Pomacentrus leucostictus* | beaugregory |
| *Epinephelus fulva* | coney | *Pomacentrus variabilis* | cocoa damselfish |
| *Epinephelus striatus* | Nassau grouper | *Pomacentrus fuscus* | dusky damselfish |
| *Equetus acuminatus* | high-hat | *Pomacentrus partitus* | bicolor damselfish |
| *Equetus lanceolatus* | jacknife fish | *Pomacentrus planifrons* | threespot damselfish |
| *Equetus punctatus* | spotted drum | *Pseudupeneus maculatus* | spotted goatfish |
| *Gerres cinereus* | yellowfin mojarra | *Pterois volitans* | lionfish |
| *Gramma loreto* | fairy basslet | *Scarus coeruleus* | blue parrotfish |
| *Haemulon aurolineatum* | tomtate grunt | *Scarus croicensis* | striped parrotfish |
| *Haemulon carbonarium* | Caesar grunt | *Scarus guacamaia* | rainbow parrotfish |
| *Haemulon chrysargyreum* | smallmouth grunt | *Scarus taeniopterus* | princess parrotfish |
| *Haemulon flavolineatum* | French grunt | *Scarus vetula* | queen parrotfish |
| *Haemulon macrostomum* | Spanish grunt | *Serranus baldwini* | lantern bass |
| *Haemulon melanurum* | cottonwick grunt | *Serranus tabacarius* | tobacco fish |
| *Haemulon plumierii* | white grunt | *Serranus tigrinus* | harlequin bass |
| *Haemulon sciurus* | blue striped grunt | *Serranus tortugarum* | chalk bass |
| *Haemulon sp. unidentified* | unidentified grunt | *Sparisoma atomarium* | greenblotch parrotfish |
| *Haemulon striatum* | striped grunt | *Sparisoma aurofrenatum* | redband parrotfish |
| *Halichoeres bivittatus* | slippery dick | *Sparisoma chrysopterum* | redtail parrotfish |
| *Halichoeres cyanocephalus* | yellowcheek wrasse | *Sparisoma radians* | bucktooth parrotfish |
| *Halichoeres garnoti* | yellowhead wrasse | *Sparisoma rubripinne* | yellowtail parrotfish |
| *Halichoeres maculipinna* | clown wrasse | *Sparisoma viride* | stoplight parrotfish |
| *Halichoeres pictus* | rainbow wrasse | *Sphoeroides dorsalis* | marbled puffer |
| *Halichoeres poeyi* | blackear wrasse | *Sphoeroides spengleri* | bandtail puffer |
| *Halichoeres radiatus* | puddingwife | *Synodus intermedius* | sand diver |
| *Holacanthus ciliaris* | queen angelfish | *Synodus saurus* | bluestripe lizardfish |
| *Holacanthus tricolor* | rock beauty | *Synodus synodus* | red lizardfish |
|  |  | *Thalassoma bifasciatum* | bluehead wrasse |

Table A.2. Benthic species included in richness calculations. \* indicates recognizable taxonomic unit.

|  |  |
| --- | --- |
| **Coral species** | **Sponge species** |
| *Acropora cervicornis* | *\*Agelas citrina*, *Agelas clathrodes*, or *Clathria faviformis* |
| *Acropora palmata* | *Agelas conifera* |
| *Agaricia agaricites* | *\*Agelas* spp. |
| *\*Agaricia* spp. (mostly *Agaricia humilis* | *\*Aiolochroia crassa* and *Verongula rigida* |
| and *Agaricia lamarcki*) | *Amphimedon compressa* |
| *Cladocora arbuscula* | *\*Amphimedon* sp. (maybe *Amphimedon complanata*) |
| *Colpophyllia natans* | *Amphimedon viridis* |
| *Dendrogyra cylindrus* | *\*Aplysina fistularis*, *Aplysina fulva*, and *Aplysina insularis* |
| *Diploria labyrinthiformis* | *Aplysina cauliformis* |
| *\*Diploria strigosa* and *Diploria clivosa* | *\*Aplysina lacunosa*, *Suberea* sp., and *Verongula reiswigi* |
| *Dichocoenia stokesi* | *\*Artemisina melana* or *Iotrochota arenosa* |
| *Eusmilia fastigiata* | \*Black, spiny, purple exudate, but not slimy |
| *Favia fragum* | \*Breadcrumb (*Calyx podatypa*, *Svenzea* |
| *Helioceris cucullata* | *cristinae*, or *Svenzea zeai*) |
| *Isophyllia sinuosa* | *Callyspongia fallax* |
| *Manicina areolata* | \*Like *Callyspongia fallax* but soft with pinched tube ends |
| *Montastraea cavernosa* | *Callyspongia plicifera* |
| *\*Madracis mirabilis* and *Madracis decactis* | *Callyspongia vaginalis* |
| *Meandrina meandrites* | *Cervicornia cuspidifera* |
| *\*Montastraea annularis, M. franksi, M. faveolata* | *Chondrilla caribensis* |
| (genus name now Orbicella) | *Cinachyrella kuekenthali* |
| *Mussa angulosa* | *Clathria venosa* |
| *\*Mycetophyllia ferox, Mycetophyllia lamarckiana* | *Clathria virgultosa* |
| *\*Oculina* spp. | *Cliona delitrix* |
| *Porites astreoides* | *Cliona laticavicola* |
| *Porites colonensis* | *Cliona varians* |
| *Porites furcata* | *\*Cribochalina vasculum* and *Petrosia pellasarca* |
| *Porites porites* | *Desmapsamma anchorata* |
| *\*Scolymia* spp. | *Dictyonella funicularis* |
| *\*Siderastrea siderea* and *Siderastrea radians* | *Dragmacidon reticulatum* |
| *Solenastrea bournoni* | *Dysidea janiae* |
| *Stephanocoenia intersepta* | *\*Dysidea* sp. (maybe etheria) |
|  | *Ectyoplasia ferox* |
|  | *Halisarca caerulea* |
|  | *\*Higginsia coralloides* (may include *Ptilocaulis walpersii*) |
|  | *\*Hyrtios* sp. or *Spheciospongia vesparium* |
|  | *Iotrochota birotulata* |
|  | *\*Iotrochota* sp. |
|  | *Ircinia campana* |
|  | *Ircinia felix* |
|  | *Ircinia strobilina* |
|  | \*Maybe "Ircinia smooth" or Spongia |
|  | *Monanchora arbuscula* |
|  | *Mycale laevis* |
|  | *Mycale laxissima* |
|  | *Neofibularia nolitangere* |
|  | *\*Neopetrosia proxima* (may include |
|  | *Xestospongia subtriangularis*) |
|  | *\*Niphates erecta* (may include *Niphates amorpha*) |
|  | *\*Niphates* sp. or *Lissodendoryx* sp.? |
|  | \*Orange encrusting |
|  | *Pandaros acanthifolium* |
|  | *\*Plakortis* sp. |
|  | \*Red Encrusting |
|  | *Scopalina ruetzleri* |
|  | *\*Spirastrella coccinea* and *Spirastrella hartmani* |
|  | *Spongosorites coralliphaga* |
|  | *Tectitethya crypta* |
|  | \*Unidentified |
|  | *Xestospongia muta* |

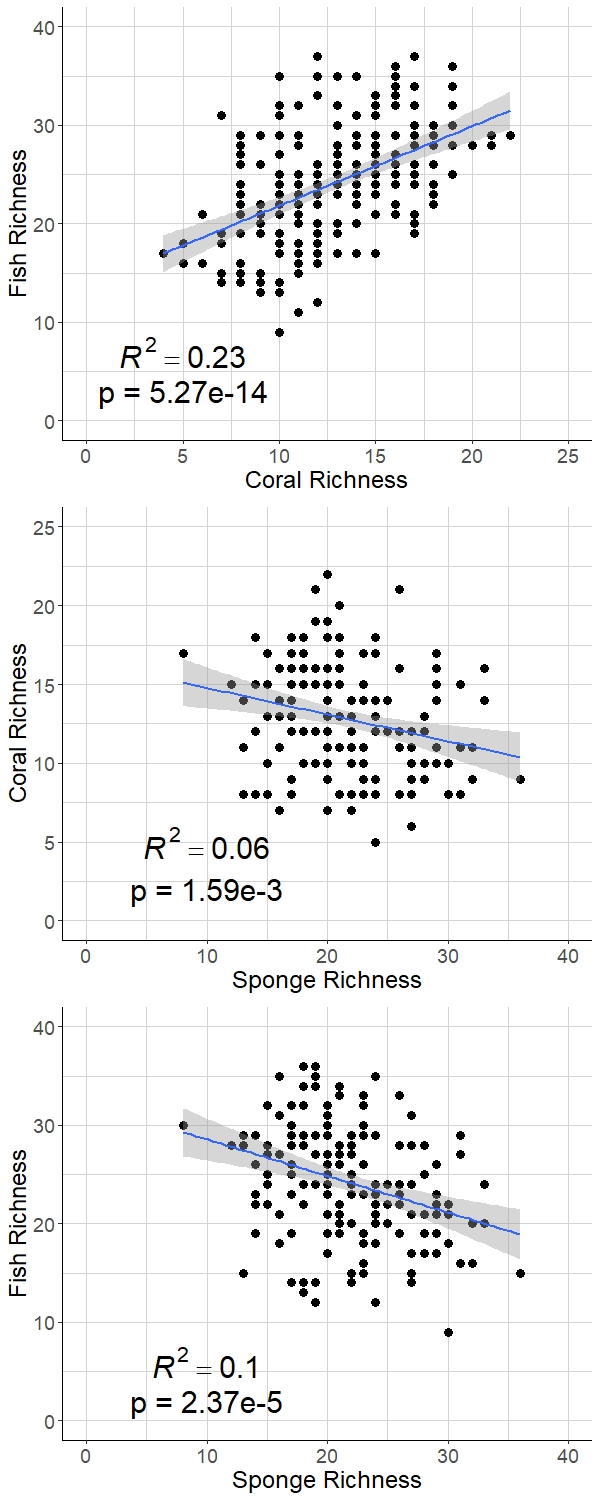


Figure A.3. Basic associations between the targets. Lines represent smoothed conditional means using a generalized linear model and the formula y ~ x. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared (*R*2) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

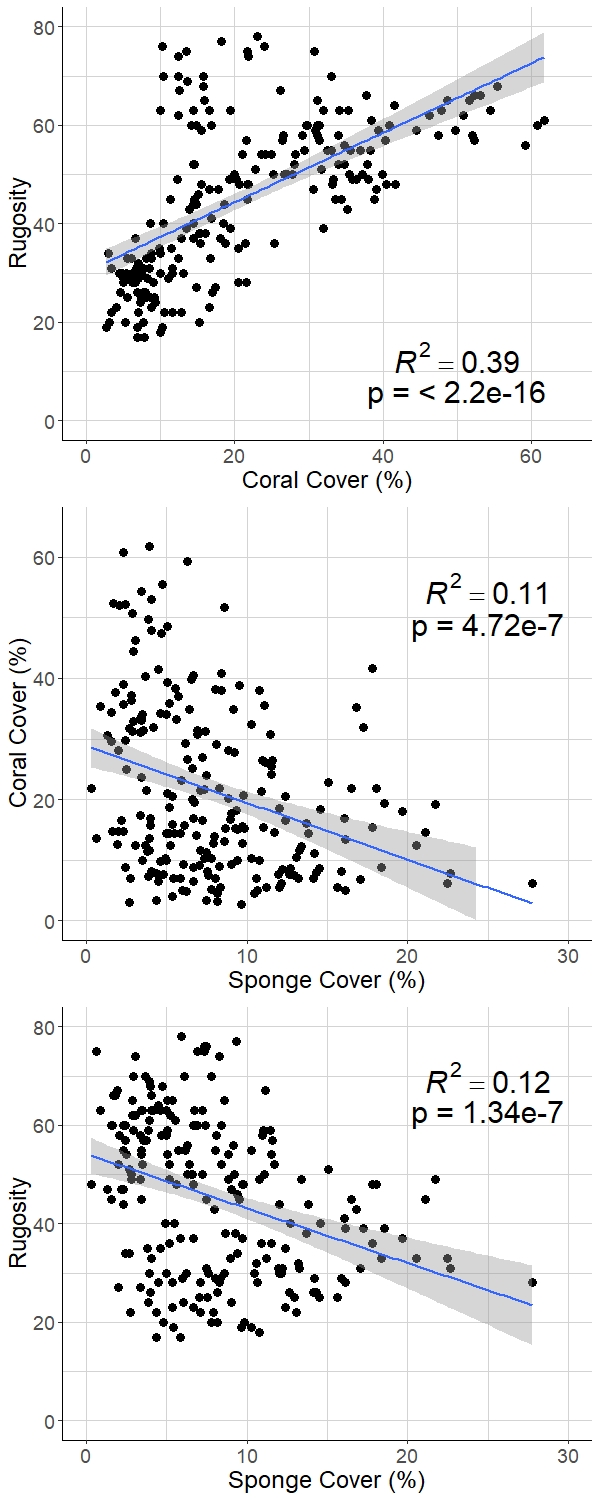


Figure A.4. Basic associations between the surrogates. Lines represent smoothed conditional means using a generalized linear model and the formula y ~ x. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared (*R*2) and p-values are shown. Rugosity measured in centimeters. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

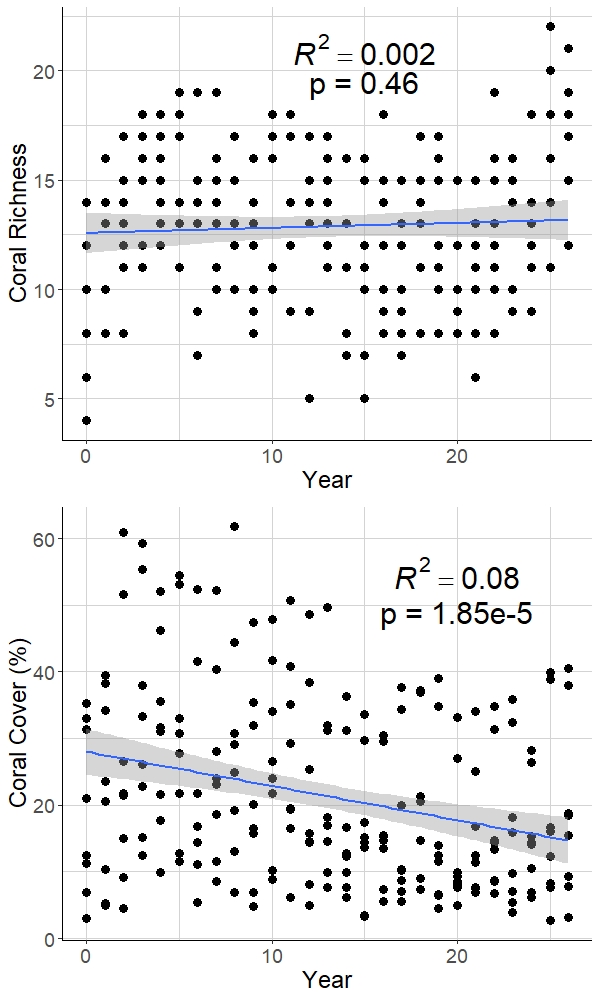


Figure A.5. Coral richness and coral cover over the 27 year study period from 1992-2018, where year 0 is 1992. Lines represent smoothed conditional means using a generalized linear model and the formula y ~ x, where x is year as a trend. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared (*R*2) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI.

Appendix 6. Model output for the most competitive model for predicting coral richness including a term for year. Estimates calculated using the negative binomial distribution and the formula y ~ x + year, where y coral richness, x is coral cover, and year is a trend. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 2.0751 0.0571 36.350 < 2e-16 \*\*\*

Percent\_Coral\_Cover 0.0152 0.0013 11.275 < 2e-16 \*\*\*

Year 0.0103 0.0026 4.012 6.03e-05 \*\*\*

---

Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix 7. Model output for the most competitive model for predicting coral richness including terms for year and the interaction between coral cover and year. Estimates calculated using the negative binomial distribution and the formula y ~ x + year + x \* year, where y coral richness, x is coral cover, and year is a trend. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 2.1163 0.0757 27.950 < 2e-16 \*\*\*

Percent\_Coral\_Cover 0.0136 0.0024 5.763 8.25e-09 \*\*\*

Year 0.0070 0.0048 1.478 0.139

Percent\_Coral\_Cover:Year 0.0001 0.0002 0.823 0.411

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Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix 8. Model output for the most competitive model for predicting sponge richness including terms for year and site. Estimates calculated using the negative binomial distribution and the formula y ~ x + year + site, where y is sponge richness, x is coral cover, year is a trend, and site is a categorical predictor. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 3.0204 0.0901 33.511 < 2e-16 \*\*\*

Percent\_Coral\_Cover 0.0041 0.0029 1.443 0.148955

Year 0.0106 0.0027 3.885 0.000102 \*\*\*

Sitecrab -0.3709 0.0688 -5.392 6.95e-08 \*\*\*

Sitegrand -0.0802 0.0628 -1.276 0.201957

Siteiguana -0.3964 0.0964 -4.110 3.96e-05 \*\*\*

Sitemonkey 0.1110 0.0671 1.655 0.097956 .

SitemuskN -0.4417 0.0862 -5.124 2.99e-07 \*\*\*

Sitepelican -0.0650 0.0694 -0.937 0.348668

Sitewhite -0.3335 0.0673 -4.957 7.16e-07 \*\*\*

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Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix 9. Model output for the most competitive model for predicting fish richness including terms for site. Estimates calculated using the negative binomial distribution and the formula y ~ x + site, where y is fish richness, x is rugosity in cm, and site is a categorical predictor. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 3.0322 0.0908 33.394 < 2e-16 \*\*\*

Rugosity 0.0024 0.0019 1.309 0.190702

Sitecrab 0.1161 0.0552 2.103 0.035468 \*

Sitegrand 0.0932 0.0706 1.321 0.186509

Siteiguana 0.2199 0.0575 3.822 0.000132 \*\*\*

Sitemonkey -0.1508 0.0648 -2.325 0.020081 \*

SitemuskN 0.2524 0.0600 4.206 2.60e-05 \*\*\*

Sitepelican -0.3540 0.0739 -4.790 1.67e-06 \*\*\*

Sitewhite -0.0193 0.0572 -0.337 0.736017

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Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix 10. Model output for the most competitive model for predicting combined richness, as the sum of coral, fish, and sponge richness, including terms for year and site. Estimates calculated using the negative binomial distribution and the formula y ~ x + year + site, where y is combined richness, x is rugosity in cm, year is a trend, and site is a categorical predictor. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

Estimate Std. Error z value Pr(>|z|)

(Intercept) 3.8663 0.0991 39.023 < 2e-16 \*\*\*

Rugosity 0.0043 0.0018 2.383 0.017150 \*

Year 0.0052 0.0017 3.002 0.002678 \*\*

Sitecrab -0.0706 0.0418 -1.690 0.090956 .

Sitegrand -0.0986 0.0594 -1.659 0.097162 .

Siteiguana 0.0016 0.0434 0.037 0.970659

Sitemonkey -0.0275 0.0469 -0.587 0.556993

SitemuskN -0.0314 0.0474 -0.661 0.508411

Sitepelican -0.1573 0.0565 -2.783 0.005388 \*\*

Sitewhite -0.1422 0.0423 -3.366 0.000764 \*\*\*

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Significance codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

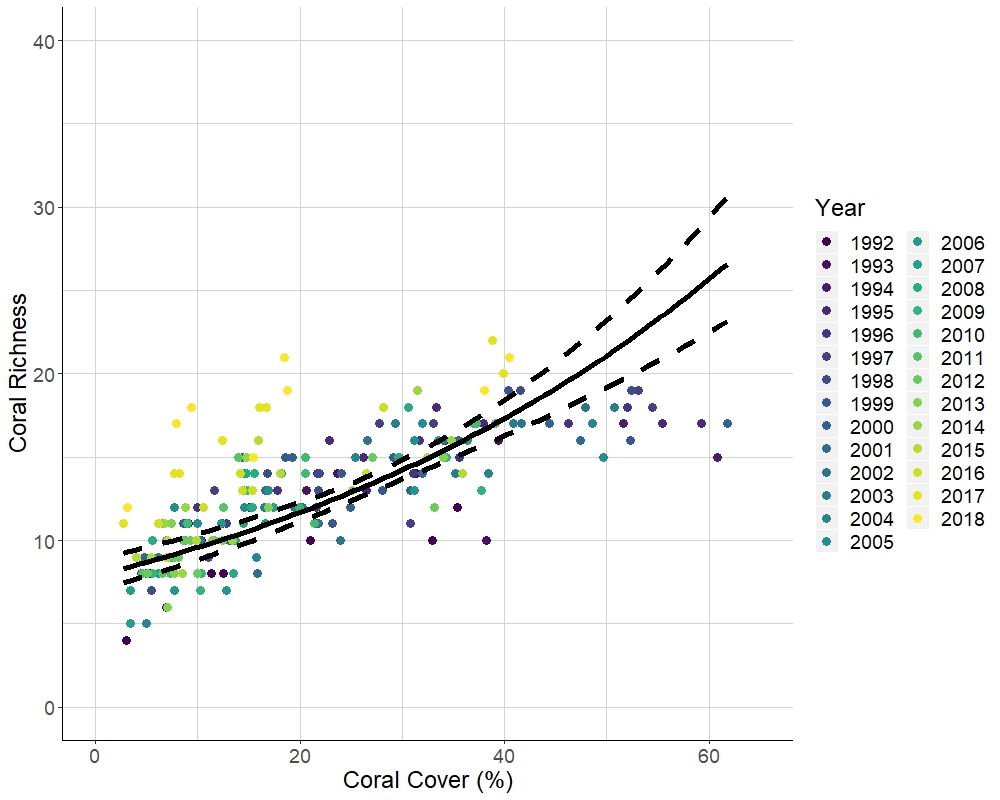


Figure #. Competitive models for predicting coral richness included a term for year. Solid line represents predictions using the negative binomial distribution and the formula y ~ x + year, where y coral richness, x is coral cover, and year is a trend. Dashed lines represent 95% confidence intervals of fitted values. Points represent observed values colored by year. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

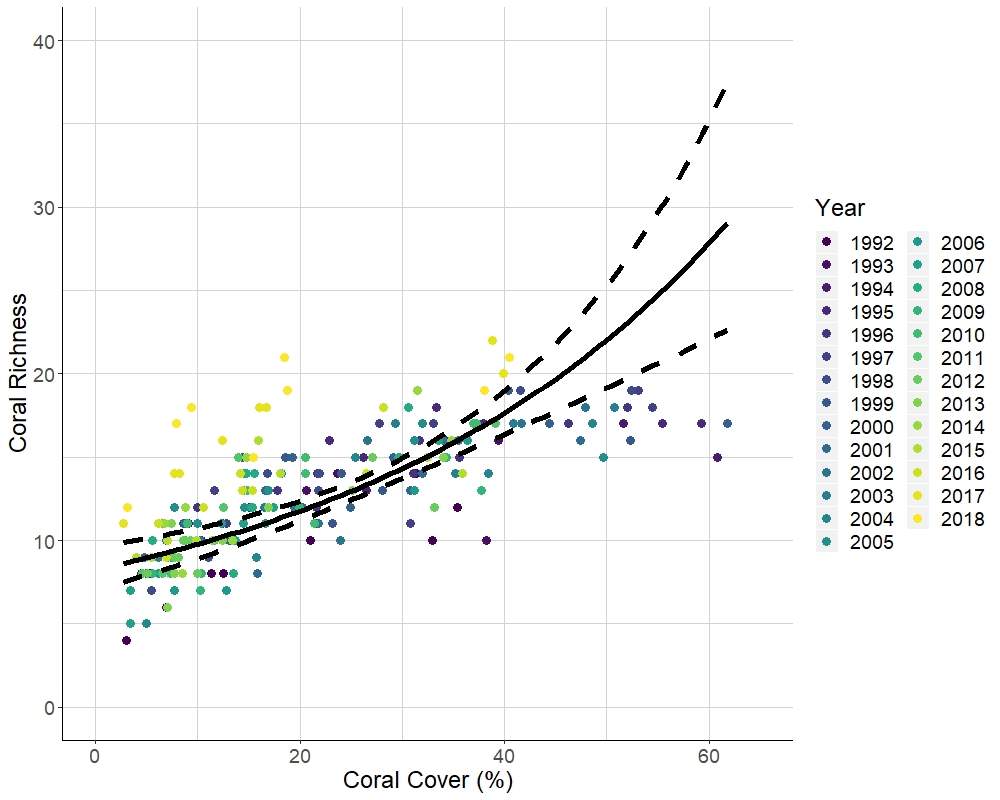


Figure #. Competitive models for predicting coral richness included a term for year. Solid line represents predictions using the negative binomial distribution and the formula y ~ x + year + x \* year, where y coral richness, x is coral cover, and year is a trend. Dashed lines represent 95% confidence intervals of fitted values. Points represent observed values colored by year. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

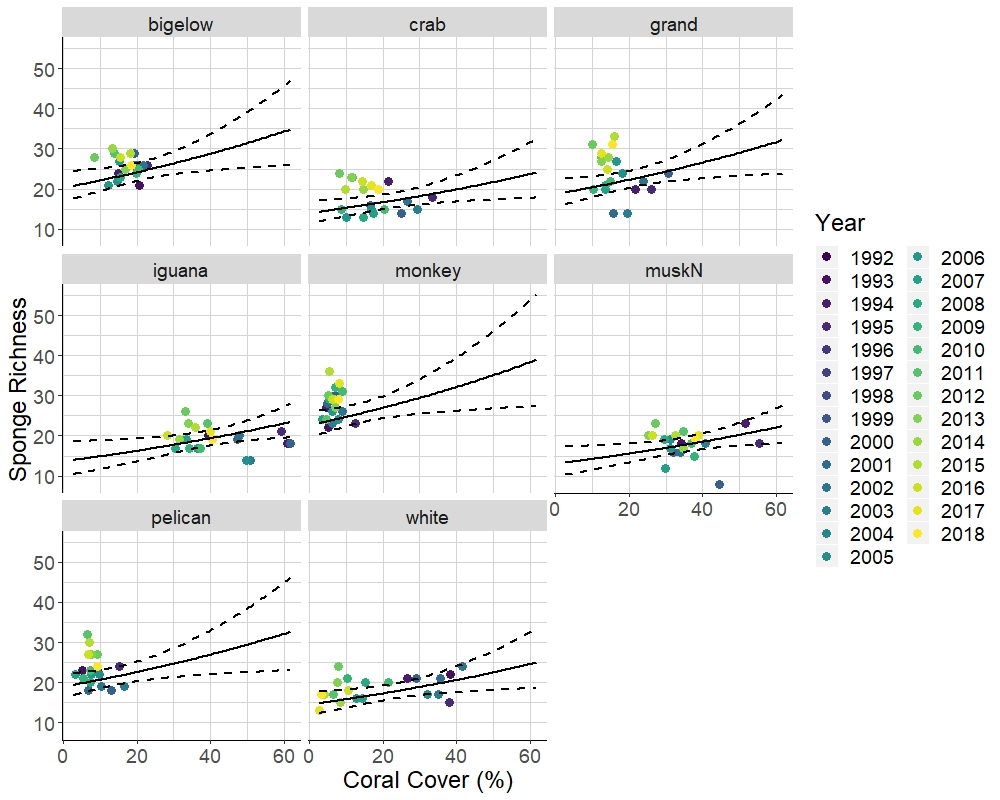


Figure #. The most competitive model for predicting sponge richness included terms for year and site. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid lines represent predictions using the negative binomial distribution and the formula y ~ x + year + site, where y is sponge richness, x is coral cover, year is a trend, and site is a categorical predictor. Dashed lines represent 95% confidence intervals of fitted values. Points represent observed values colored by year. Data were collected from 1992-2018.

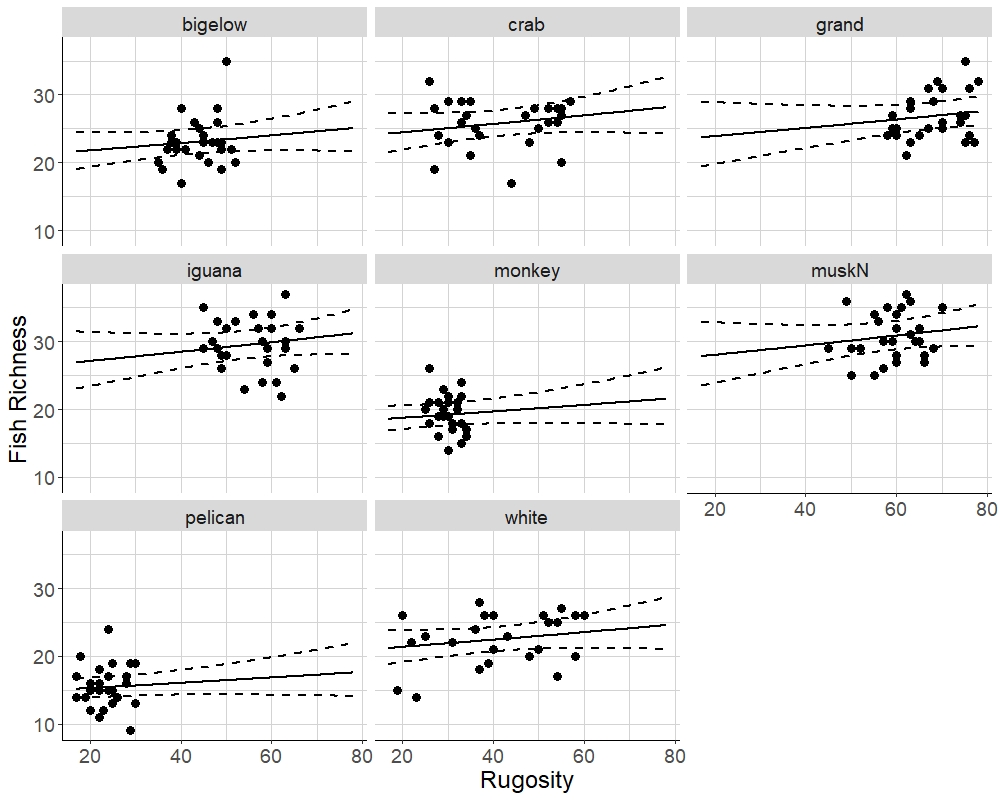


Figure #. The most competitive model for predicting fish richness included a term for site. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid lines represent predictions using the negative binomial distribution and the formula y ~ x + site, where y is fish richness, x is rugosity in cm, and site is a categorical predictor. Dashed lines represent 95% confidence intervals of fitted values. Points represent observed values. Data were collected from 1992-2018.

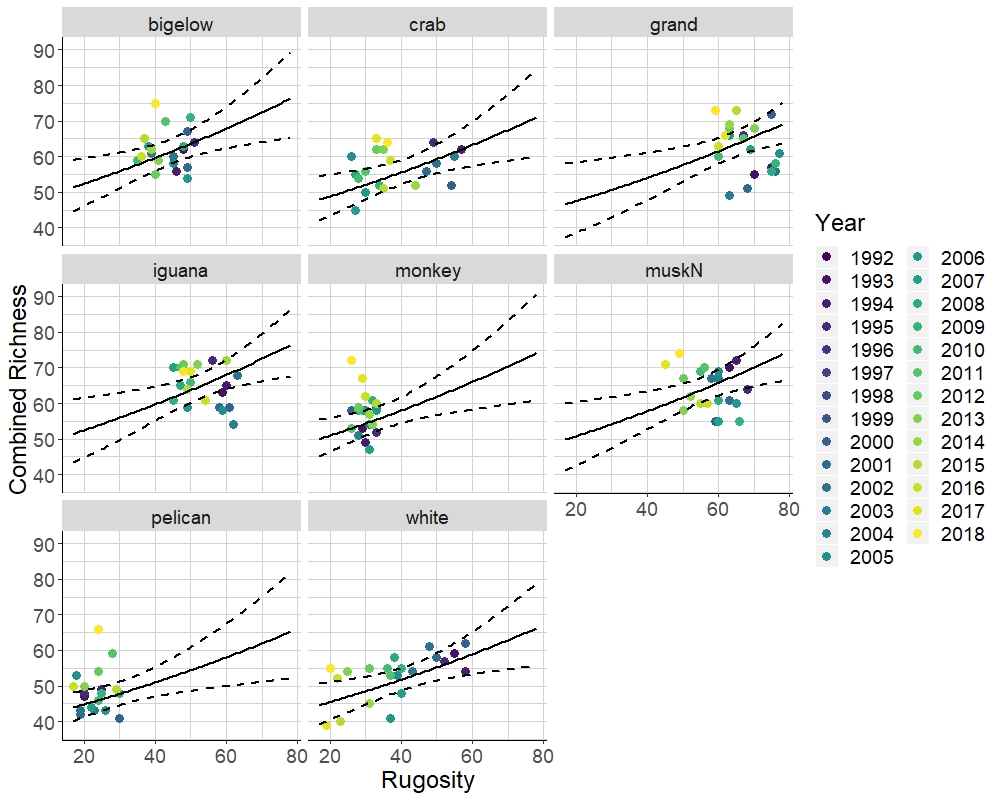


Figure #. The most competitive model for predicting combined richness, as the sum of coral, fish, and sponge richness, included terms for year and site. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid lines represent predictions using the negative binomial distribution and the formula y ~ x + year + site, where y is combined richness, x is rugosity in cm, year is a trend, and site is a categorical predictor. Dashed lines represent 95% confidence intervals of fitted values. Points represent observed values colored by year. Data were collected from 1992-2018.

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