remote sensing

Technical Note

Structural Complexity of Coral Reefs in Guam, Mariana Islands

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Abstract: The complexity of tropical reef habitats affects the occurrence and diversity of the organisms residing in these ecosystems. Quantifying this complexity is important to better understand and monitor reef community assemblages and their roles in providing ecological services. This study employed structure-from-motion photogrammetry to produce accurate 3D reconstructions of eight reefs in Guam and quantified the structural complexity of these sites using seven terrain metrics: rugosity, slope, vector ruggedness measure (VRM), multiscale roughness (magnitude and scale), plan curvature, and profile curvature. The relationships between terrain complexity, benthic community diversity, and coral cover were investigated with generalized linear models. While the average structural complexity metrics did not differ between most sites, there was significant variation within sites. All surveyed transects exhibited high structural complexity, with an average rugosity of 2.28 and an average slope of 43 degrees. Benthic diversity was significantly correlated with the roughness magnitude. Coral cover was significantly correlated with slope, roughness magnitude, and VRM. This study is among the first to employ this methodology in Guam and provides additional insight into the structural complexity of Guam's reefs, which can become an important component of holistic reef assessments in the future.

Keywords: structure from motion (SfM); coral reefs; Guam; habitat complexity; marine monitoring; benthic surveys; coral reef topography

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1. Introduction

Recent technological advances have revolutionized the way that researchers can observe, study, and understand reef composition and ecology. Innovations in imaging, optics, and 3D data processing have made this technology more affordable and accessible than ever before [1,2]. In community ecology, form and function have long been recognized as strongly associated with one another [3,4]. A strong relationship exists between the structural complexity of habitats and their species diversity across various ecosystems [5–8].

Shallow-water tropical reefs can harbor high degrees of biodiversity and structural complexity [9–12]. The diverse array of biotic organisms and abiotic structures that comprise reefs are often organized in complex arrangements of microhabitats that house a diversity of fish and invertebrate species [13,14]. Structural complexity plays a major role in coral reef ecosystem function and has been found to influence several factors, including reef fish and sessile vertebrate assemblages, species richness, and recovery from disturbance [14–17]. A reef's three-dimensional structure has also been shown to determine its resistance to the effects of climate change [18]. Moreover, reef structural complexity can benefit coastal protection in the face of rising sea levels [19]. Enhancing structural complexity also has the potential to improve reef restoration efforts [20]. The multitude of factors influenced by the structural complexity of tropical reefs makes its quantification important to both better understand reef ecology and manage reef health.

In addition to being the most biodiverse marine ecosystem on Earth, tropical reefs are also among the most ecologically and economically productive [21,22]. Reef health is in decline globally due to a combination of global, regional, and local stressors [23–25] as exemplified by decreasing coral cover and the degradation of reef habitats [26,27]. The loss of live coral cover has led to drastic declines in reef structural complexity, which is expected to affect reef biodiversity in the coming decades [28–30]. This phenomenon, coined 'coral reef flattening' [31], is considered a potential precursor to the functional collapse of coral reef ecosystems [32]. Consequently, structural complexity might serve as a proxy for several variables that describe different aspects of reef health (e.g., benthic community composition, habitat quality, etc.) and can be used to document changes in reef health [8].

As such, measuring the 3D structural complexity of reefs has garnered significant interest in recent years [1,2,33]. The metric most frequently used to quantify 3D structures is rugosity, a scale-dependent measure of complexity that can be defined as the ratio between the contour length (or area) along the terrain and the planar distance (or area) of the surface [10,34–36]. Two other metrics of terrain variability, roughness and ruggedness, have also been used with increasing frequency in recent years [13,37–40]. While there are several ways of determining roughness and ruggedness, they all generally describe variability in elevation within a spatial unit [41]. In addition to rugosity, roughness, and ruggedness, more than 20 other metrics of terrain change have been linked to variations in benthic and fish community assemblages [10,17,42,43]. Efforts to quantify these metrics have historically been undertaken manually, and in situ measurements of rugosity and other metrics have been conducted for over half of a century [44]. However, in addition to being time-consuming and prone to user error, these traditional methods are impractical when measuring large areas and can damage benthic organisms [45]. This has led researchers to explore faster, more accurate, and less harmful alternative methods, which has been facilitated by advances in imaging, remote sensing, and other data collection technologies [40,46].

One such approach that has garnered increased interest involves the use of structure-from-motion (SfM) photogrammetry, which uses the overlap between photographs and parallax and allows for the use of 2D data to produce 3D reconstructions [47]. SfM is a rapid, cost-effective technique that has the potential to alleviate the aforementioned issues associated with traditional survey methods [42,48,49]. SfM has been shown to effectively quantify structure at scales ranging from individual coral colonies to entire reef sites [36,45,50,51]. It has also been used to quantify the influence of structural complexity on fish communities, the rate of coral growth and reef accretion, the effect of coral colony morphology on structural complexity, and changes in structural complexity following disturbance events [39,42,51–54]. The use of SfM to accurately reconstruct reef topography and quantify structural complexity was the main objective of this study, where SfM was used to quantify various terrain metrics for eight reefs around Guam.

Guam (13°28′N, 144°46′E) is located just outside of the Indo-Pacific center of reef biodiversity [55] and is home to more than 5000 documented marine species, making it one of the most diverse and speciose nearshore marine ecosystems of all US jurisdictions [56–59]. Despite possessing significant economic, cultural, and ecological value to the island, the health of Guam's reefs has been in decline since the 1960s [60]. This trend has accelerated since 2013 following a succession of severe environmental disturbances, including extreme low tides from 2014–2015 triggered by an El Niño Southern Oscillation (ENSO) event, as well as severe island-wide bleaching events in 2013, 2014, 2016, and 2017 [61,62]. This sequence of events resulted in a 34–37% decline in island-wide coral cover [61,62] and notable changes in benthic community composition [63,64]. The declining health of Guam's reefs has made the need for monitoring more pressing than ever. The structural complexity of Guam's reefs should be monitored in addition to the community composition to better understand the correlation between structural complexity, biodiversity [7], community composition, and coral cover [28,30]. In addition to providing one of the first topographic characterizations of a selection of Guam's reefs using SfM, the relationships between habitat complexity and benthic community composition and coral cover were also investigated for each site.

2. Materials and Methods

2.1. Study Area

Structure-from-motion (SfM) photogrammetry was conducted in eight reefs in western and northeastern Guam (Figure 1) in October 2019. The surveyed reefs were nearshore, shallow-water reefs between 8 and 12 m in depth and are influenced by a broad range of ecological and environmental factors, including wave exposure, habitat heterogeneity, and human impact [60,65,66]. SfM photogrammetry largely followed the methodology described by Leon et al. [36] and González Rivero et al. [67], with minor modifications. The modified protocols are summarized below.

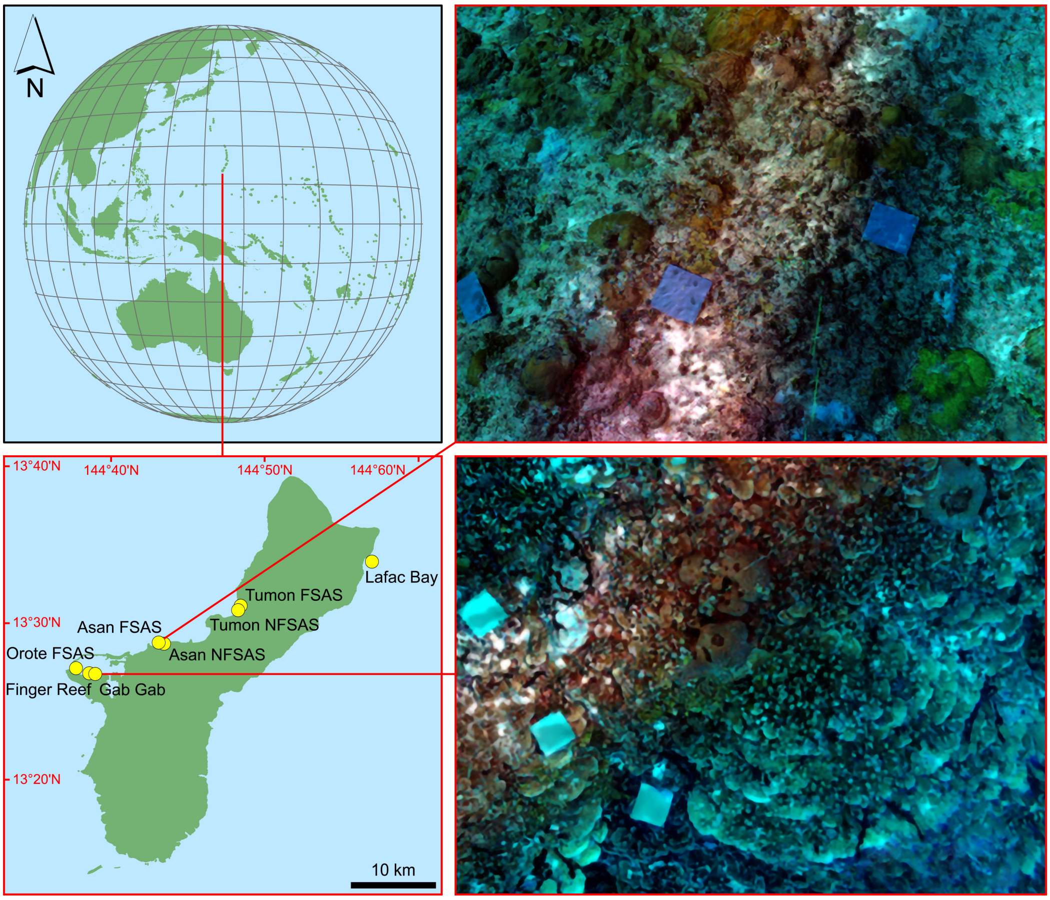

Figure 1. Map of the study area with Guam magnified to show the location of the survey sites (yellow dots). The sections on the right outlined in red show parts of surveyed transects. Scale bar = 10 km. Maps were created using ArcGIS Pro 2.9 (Esri, Redlands, CA, USA).

2.2. Structure-from-Motion Photogrammetry

SfM photogrammetry was used to survey transects on eight reefs around Guam using an array of three GoPro Hero4 cameras (GoPro Inc., San Mateo, CA, USA). The rounded lenses that come standard on these cameras were replaced with PeauPro82 3.97 mm f/2.8 GoPro lenses (Peau Productions, San Diego, CA, USA) to mitigate image radial distortion and the potential propagation of uncertainty through the image analysis [68]. In sites where permanent transects were already present, Lafac Bay (5 × 50 m transects) and Gab Gab (6 × 50 m transects), surveys were conducted using the established transects. In the remaining six sites, surveys were performed using 6 × 50 m randomly placed transects. All transects were automatically georeferenced using the DiveRay (PlanBlue GmbH, Bremen, Germany), a diver-operated hyperspectral imager that was used concurrently to conduct benthic surveys [69,70]. Cameras were rigged 50 cm apart and oriented such that photos were taken perpendicular to the bottom. The rig was used to conduct surveys 1–1.5 m above the reef, resulting in a ground sampling distance of 1.3 mm, and cameras were programmed to capture photos every half-second to ensure sufficient front and side overlaps between photos. A total of nine 10 × 10 cm matte grey reference plates per transect were used as ground control (optimization) and checkpoints (accuracy assessment). Three reference plates were placed at the beginning, middle, and end of each transect.

The SfM process produces 3D point clouds, orthomosaics, and digital surface models (DSMs) from overlapping images. For a thorough description and guidelines, readers are referred to the reviews by Smith et al. [71] and James et al. [72]. Briefly, the workflow involves (1) camera alignment; (2) bundle block adjustment; (3) the optimization of camera calibration parameters; (4) the generation of dense point clouds using multiview stereo (MVS); and (5) the generation of DSMs and orthomosaics. During the optimization step, we gradually removed approximately 10% of points from the sparse cloud that had high reconstruction uncertainty, reprojection errors, or low projection accuracy. Agisoft Metashape 2.0 (Agisoft LLC, St. Petersburg, Russia) was used for SfM processing. The derived data products consisted of orthomosaics and DSMs at a spatial resolution of 0.0003 m (0.3 mm) and 0.001 m (1 mm), respectively. Coordinates and elevation were referenced to arbitrary datums.

2.3. Data Analysis

Structural complexity metrics were calculated from the DSMs using ArcGIS Pro 2.9 (Esri, Redlands, CA, USA). DSMs were first smoothed using a low-pass filter (3 × 3 neighborhood window) and clipped using a negative 1 m buffer from the edge to remove potential artifacts and outliers. Terrain metrics, which are frequently used to quantify structural complexity and shape biotic communities on reefs or indicate ecosystem health and stability, e.g., [17,38,40,73–75], were derived from the DSMs using a 3 × 3 pixels (4 mm) neighborhood window (Table 1). The vector ruggedness measure (VRM) was also derived based on a 5 cm neighborhood window [37]. The derived metrics included the surface/area ratio (rugosity), slope, VRM, multiscale roughness magnitude and scale (hereafter referred to as the roughness magnitude and roughness scale), profile curvature, and planform (plan) curvature. Plan and profile curvature are often highly correlated when averaged across an entire reef area, leading researchers to instead examine the range or variance of these metrics [37,39]. As such, the standard deviations of both plan and profile curvature (in z units) were examined herein as a proxy for variance. The surface/area ratio (rugosity) and roughness magnitude and scale were derived using SurfaceAreaRatio and MultiscaleRoughness from Whitebox Tools, respectively [76,77]. The roughness magnitude and roughness scale are both outputs of a method designed to determine roughness at fine resolution across multiple spatial scales [77]. These metrics were used to characterize the survey sites and quantify their structural complexity (Table S1).

Table 1. Description of terrain metrics with relevant references.

Terrain Metric	Description and Relevance	References
Surface/area ratio (rugosity)	The ratio between the surface area (3D) and planar area (2D) of terrain. A long-used terrain metric in ecological reef surveys. The primary metric used to measure 'coral reef flattening'.	[31,78,79]
Slope	The degree of incline (steepness) of a surface. It is measured as the maximum rate of change in elevation between a cell and the eight cells surrounding it. An often-used metric to describe steepness, seafloor complexity, and vertical relief of reefs.	[17,80]

Table 1. *Cont.*

Terrain Metric	Description and Relevance	References
Vector ruggedness measure	Quantifies ruggedness as the variation in the 3D orientation of cells within the roving window, effectively capturing slope and aspect (direction of slope) into a single measure. A metric of seafloor complexity that is decoupled from slope or elevation, often allowing it to quantify terrain variation more independently and quantify different features of terrain than many other traditional metrics.	[40,81,82]
Roughness magnitude	The first output of MultiscaleRoughness (MR), which determines the maximum roughness value (σ_{max}) for each cell in a raster. Multiscale metrics such as MR mitigate the shortcomings associated with arbitrary scale selection.	[38,40,77]
Roughness scale	The second output of MultiscaleRoughness, which determines the filter radius (spatial scale; r) associated with the greatest roughness value that identifies the spatial scale at which σ_{max} is expressed.	[38,40,77]
Profile curvature	Curvature evaluated parallel to the slope. It indicates the direction of the maximum slope and can describe the acceleration or deceleration of benthic flow. It can be used to assess the structural dynamics of reefs and measure the structural complexity of coral species.	[39,42,73,83]
Planform (plan) curvature	Curvature evaluated perpendicular to the slope. It can be used to describe the convergence or divergence of flow and measure the structural complexity of coral species, ridges, crests, and valleys.	[39,42,73,83]

All statistical analyses were performed using R version 4.1.3 (R Core Team, Vienna, Austria) and RStudio version 2022.02.1 Build 461 (RStudio Team, Boston, MA, USA). Terrain metrics were tested using a one-way ANOVA and post hoc Tukey's honest significant difference test. The complexity metrics were tested for collinearity through the variance inflation factor prior to further analysis. The Shannon Diversity Index (H) [84], calculated using the 'diversity' function in the 'vegan' R package [85], was used to quantify the diversity of benthic communities at each site based on the photoquadrat surveys that were conducted in conjunction with the SfM surveys (Table S2) [69,70]. Scleractinian coral cover was also estimated using these photoquadrat surveys (Table S2). For each transect, photos of 0.25 m^2 quadrats were taken at intervals of one meter. The photos were then overlaid with 20 points (50 for the Lafac Bay photos). A benthic category was identified for each point to the highest possible taxonomic resolution (Table S3). To maintain identification consistency, the 106 benthic categories were consolidated into 67 benthic groups that were used to estimate the benthic diversity and coral cover for each transect (Table S3) [69,70]. The influence of the terrain metrics on the benthic community diversity and scleractinian coral cover was investigated using generalized linear models (GLMs) with a Gaussian error distribution. In these models, benthic diversity and coral cover served as the response variables, while the seven terrain metrics were the predictor variables (Table 1). Site was considered a fixed effect to evaluate the influence of complexity metrics on diversity and coral cover between sites. The models were used to plot the correlation between terrain metrics and the benthic diversity or coral cover at each site.

3. Results

The derived DSMs had a resolution of 1.3 mm, an average spatial extent of 49 m^2, and sub-centimeter precision. Seven commonly used metrics were calculated to quantify the structural complexity of eight reefs in Guam. Of those, rugosity, VRM, roughness magnitude, plan curvature, and profile curvature were largely similar between the sites (Figure 2; Table 2). Slope and roughness scale were the only metrics that significantly differed for more than two sites (Figure 2). Of the eight sites surveyed, five (Asan FSAS, Asan NFSAS, Orote FSAS, Tumon FSAS, and Tumon NFSAS) were similar to one another across nearly all terrain metrics. However, while the complexity of all sites was largely similar on average, significantly more variation was observed between transects.

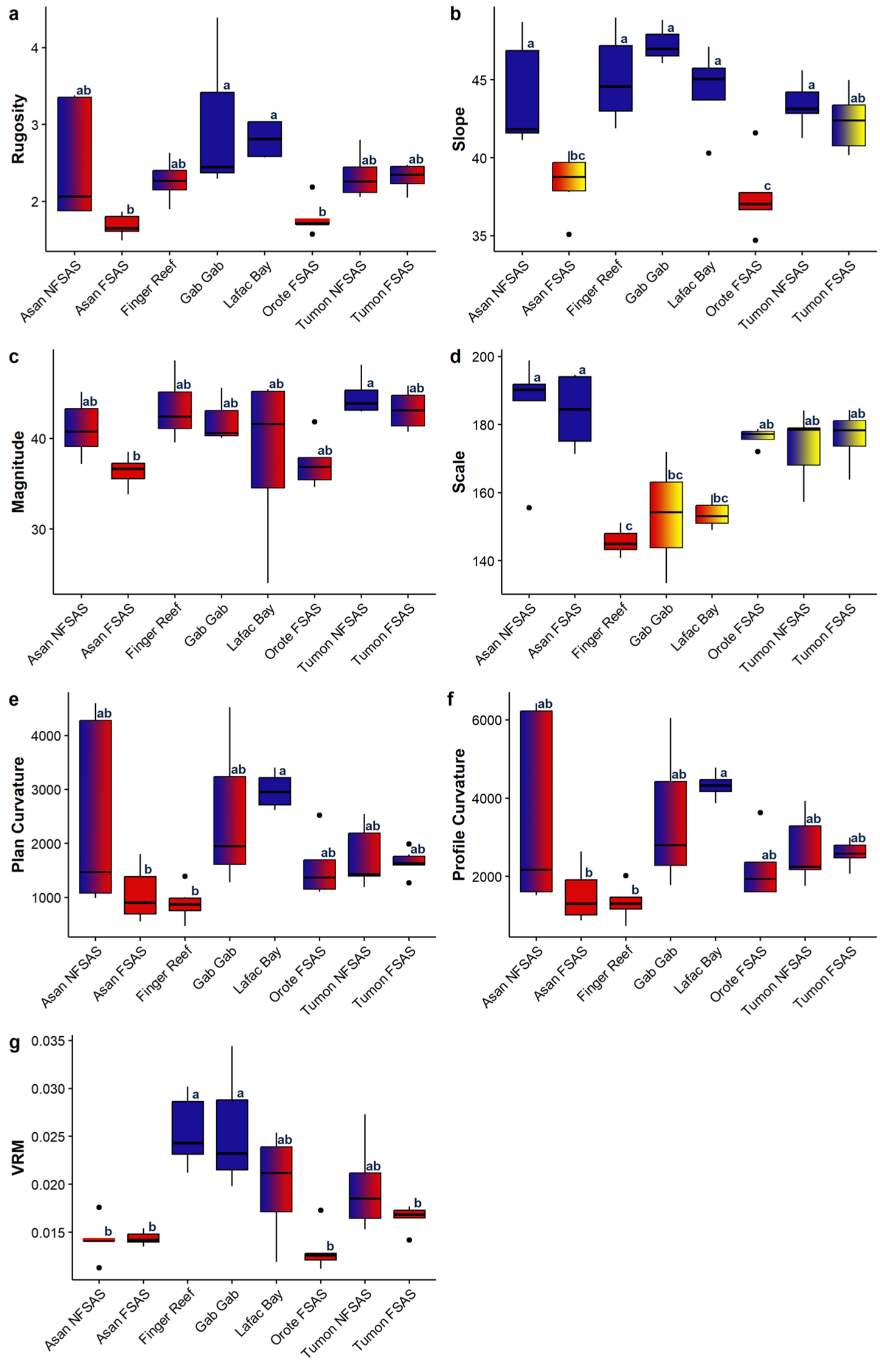

Figure 2. Box plots of terrain metrics derived from DEMs across the eight survey sites. Plots show variation between and within sites for (**a**) rugosity, (**b**) slope (°), (**c**) roughness magnitude (σ_{max}), (**d**) roughness scale (r), (**e**) plan curvature (z units), (**f**) profile curvature (z units), and (**g**) VRM. Boxes show upper and lower quartiles, horizontal lines show the median values, whiskers represent the range excluding outliers, and dots denote outliers. For each plot, the calculated terrain metric differs significantly between sites when their boxplots do not contain the same color or letter.

Table 2. Benthic community diversity, coral cover, and terrain metrics derived from DEMs for each study site. Metrics are displayed as the average of all transects ± the standard error for each site.

Site	Diversity (H)	Coral Cover (%)	Rugosity	Slope (°)	VRM	Magnitude (σ_{max})	Scale (r)	Plan Curvature (z Units)	Profile Curvature (z Units)
Asan NFSAS	1.54 ± 0.12	22 ± 3	2.51 ± 0.35	44 ± 2	0.014 ± 0.001	41.11 ± 1.42	184.70 ± 7.53	2482.85 ± 802.93	3589.53 ± 1122.11
Asan FSAS	1.26 ± 0.05	20 ± 2	1.69 ± 0.06	38 ± 1	0.014 ± 0.000	36.38 ± 0.67	184.03 ± 4.46	1056.51 ± 204.27	1528.26 ± 284.37
Finger Reef	1.27 ± 0.05	54 ± 2	2.27 ± 0.10	45 ± 1	0.025 ± 0.002	43.29 ± 1.38	145.61 ± 1.57	891.74 ± 125.04	1335.75 ± 173.00
Gab Gab	1.19 ± 0.01	57 ± 2	3.04 ± 0.67	47 ± 1	0.026 ± 0.004	42.08 ± 1.76	153.22 ± 11.12	2583.70 ± 988.53	3541.23 ± 1287.13
Lafac Bay	1.25 ± 0.07	8 ± 1	2.81 ± 0.13	44 ± 1	0.020 ± 0.003	38.15 ± 5.01	153.84 ± 3.02	2981.92 ± 181.20	4324.59 ± 187.65
Orote FSAS	0.99 ± 0.10	8 ± 1	1.78 ± 0.11	38 ± 1	0.013 ± 0.001	37.33 ± 1.26	176.30 ± 1.16	1568.27 ± 259.30	2225.05 ± 378.13
Tumon NFSAS	1.58 ± 0.08	25 ± 4	2.32 ± 0.11	43 ± 1	0.020 ± 0.002	44.60 ± 0.82	173.69 ± 4.21	1735.55 ± 241.49	2663.47 ± 363.15
Tumon FSAS	1.31 ± 0.11	7 ± 2	2.32 ± 0.07	42 ± 1	0.017 ± 0.001	43.16 ± 0.89	176.47 ± 3.02	1654.36 ± 97.20	2590.27 ± 132.90

The similarity in structural complexity at the site level was also observed when examining the effects of terrain metrics on the benthic community diversity and coral cover. After testing for collinearity, both plan and profile curvature were found to be collinear. As such, one of the metrics (profile curvature) was excluded from further analyses. Analyses indicated that the diversity of benthic communities and scleractinian coral cover were significantly related to one and three habitat complexity metrics, respectively (Figures 3 and 4). Roughness magnitude was the only significant terrain metric included in the best-fitted model for diversity (t-value = 2.78, $p = 0.01$). While diversity typically increased with increasing roughness magnitude, the effect varied between sites (Figure 3). By contrast, the best-fitted GLM for coral cover included the slope (t-value = 3.98, $p < 0.001$), roughness magnitude (t-value = −2.46, $p = 0.01$), and VRM (t-value = 3.31, $p < 0.001$). Coral cover was positively correlated with the slope, roughness magnitude, and VRM at most sites, but this relationship was not consistent across all sites (Figure 4). Overall, the similarity of structural complexity across a majority of the sites was also observed when investigating how terrain influenced coral cover and benthic diversity.

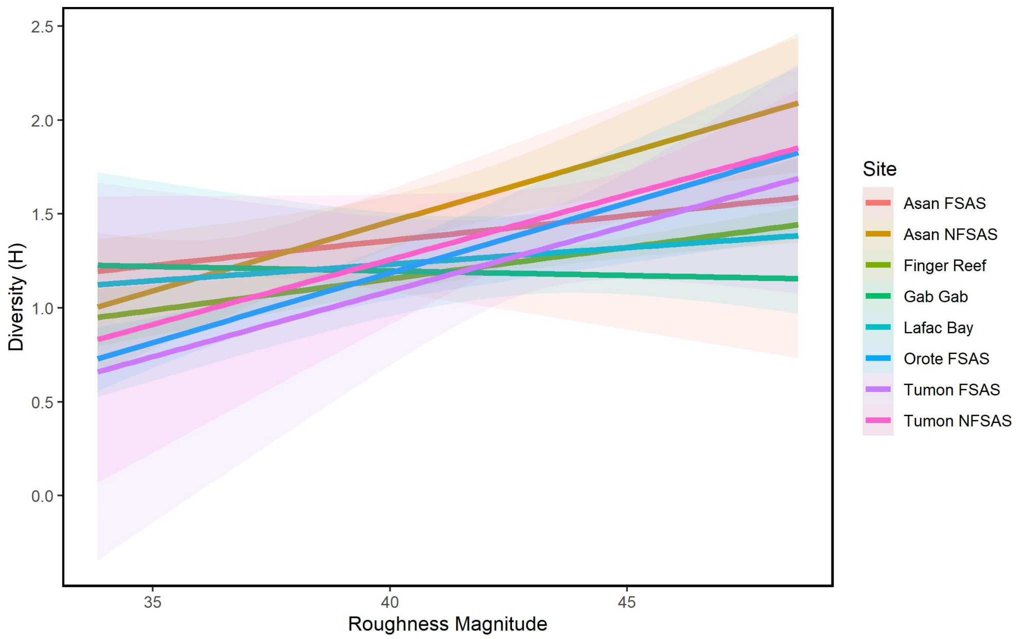

Figure 3. General linear model showing the statistically significant relationship between roughness magnitude and benthic community diversity for each site ($p < 0.05$). Sites are color-coded. Solid regression lines are predicted from the linear model, and shaded areas denote the 95% confidence intervals of the models.

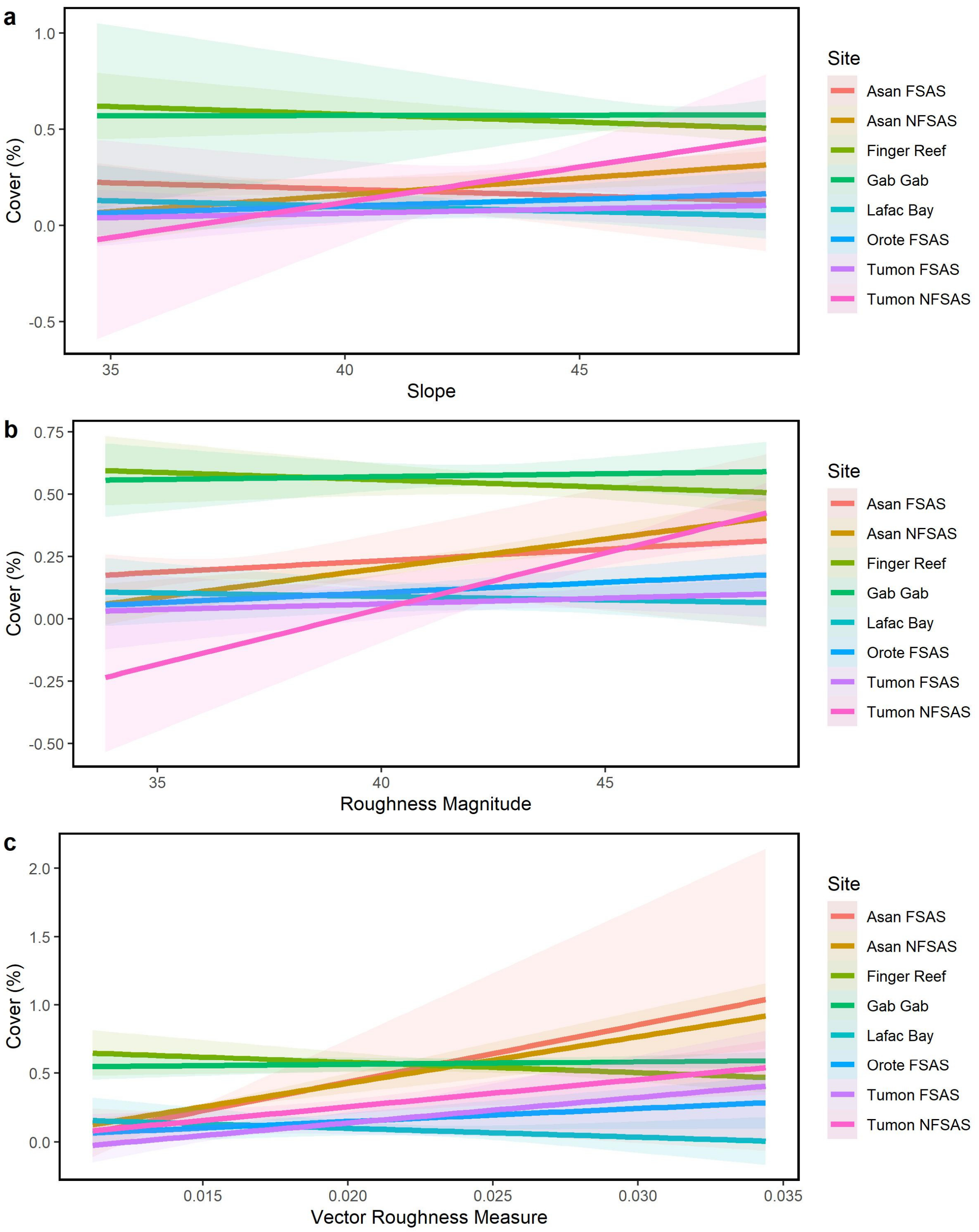

Figure 4. General linear models showing statistically significant relationships between coral cover and terrain metrics ($p < 0.05$): (**a**) GLM showing the relationship between slope and percent coral cover for each site; (**b**) GLM showing the relationship between roughness magnitude and coral cover for each site; (**c**) GLM showing the relationship between VRM and coral cover for each site. Sites are color-coded. Solid regression lines are predicted from the linear model, and shaded areas denote the 95% confidence intervals of the models.

4. Discussion

Traditional complexity metrics to describe coral reefs (e.g., rugosity, slope, plan curvature, etc.) are often correlated with each other [15]. Individual terrain metrics do not comprehensively describe the structural complexity of reefs in their entirety [86], warranting the need for a combination of terrain metrics to adequately characterize this complexity. On average, the structural complexity was similar across nearly all surveyed sites. Rugosity, the most frequently used metric to quantify structural complexity [10,34,35], ranged from 1.49 to 4.39 and averaged 2.28 across all transects, which is higher than the rugosity values reported in recent studies in Australia, the Philippines, Puerto Rico, Hawaii, and the Gulf of Mexico [15,36,42,45,74]. The slope, which ranged from 35 to 49 degrees (average of 43 degrees), was similar to that of mesophotic reefs in the southwestern Gulf of Mexico [74] and was steeper than the values that have been reported from other shallow-water reefs in Puerto Rico and Australia [15,35]. Overall, the high structural complexity measured in Guam's reefs could suggest that the reefs have been able to retain much of their complexity despite the significant decline in coral cover in recent years [61,62]. Since the maintenance or enhancement of structural complexity has the potential to improve reef restoration efforts [20], the complexity of Guam's reefs can assist in the potential future reef recovery or restoration efforts. The surveys for this study were focused on a specific depth range (8–12 m). Since depth has been found to be a factor affecting complexity [74], surveys at a range of depth stations will provide a better picture of the variation in structural complexity across depth zones.

The analysis of the seven terrain metrics (rugosity, slope, VRM, roughness magnitude, roughness scale, plan curvature, and profile curvature) revealed that there were differing effects of terrain on reef diversity and coral cover. While terrain metrics were largely similar among the sites, significant variations in these metrics were observed within sites. This suggests that measures of structural complexity are relevant at scales smaller than the site level (i.e., less than 250 m linear length along isobaths). Similar observations have been made in other studies, where scales as small as individual coral colonies have been shown to significantly influence reef structure and complexity [8,49,51,87]. However, with the exception of Lafac Bay (Figure 1, northeastern yellow dot), the survey sites were located in the center of Guam's east coast. While the effects of terrain metrics on benthic diversity and coral cover were largely similar, they were not consistent across all sites, suggesting that surveying additional sites elsewhere around the island may reveal a greater variation in terrain metrics and structural complexity.

When modeled irrespective of site, the benthic community diversity was shown to be positively correlated with the roughness magnitude (Figure S1), and this generally remained the case when modeling the diversity and roughness magnitude across the sites (Figure 3). However, collective properties such as diversity indices likely do not sufficiently demonstrate the response patterns across environmental or structural gradients [88,89], primarily because they cannot account for species- or group-specific dynamics. This has been reflected in several studies reporting the structural complexity to be negatively correlated with groups such as macroalgae and sea urchins, while positively correlated with coral cover and fish assemblages [10,53,80,90], emphasizing the need to investigate these relationships separately for different biotic groups. Coral cover was found to be positively correlated with the roughness magnitude, slope, and VRM when modeled irrespective of site (Figure S2), and these relationships remained largely the same when examining differences between sites (Figure 4). Roughness magnitude, by definition, can be increased significantly by the presence of complex features found in areas of high coral cover, biomass, and biodiversity [40,91,92]. The reefs surveyed herein exhibited high structural complexity and were composed of complex structures (e.g., spur and groove formations and live corals), reinforcing the positive correlation observed between the roughness magnitude and both the benthic diversity and coral cover across nearly all sites.

The positive correlation between coral cover and slope at most sites is in contrast with a recent study on Guam conducted by Ferreira et al. [93], which reported the opposite relationship. These contrasting findings can, in part, be explained by the difference in spatial coverage between the two studies. Most of the plots studied by Ferreira et al. [93] were placed on reefs that are dominated by *Porites rus* (communities of low macrobenthic species richness) and situated along steep reef slopes. Incidentally, Finger Reef, one of the two sites at which coral cover was negatively correlated with the slope (as well as VRM and roughness magnitude), possesses a similar community as those found in the plots investigated by Ferreira et al. [93]. Interestingly, another reef that is shaped and dominated by *P. rus* colonies (Gab Gab) was positively correlated with all three significant terrain metrics, indicating that the negative relationship between the slope and coral cover is not consistent across sites with comparable biological communities. The other site where coral cover and the three terrain metrics were negatively correlated was Lafac Bay, which has experienced significant coral mortality since 2017 [69]. The sites investigated in this study covered a broader range of benthic communities [69,70]. Furthermore, while Ferreira et al. [93] examined 4 m^2 plots, we measured the complexity and coral cover over ~50 m^2 transects. This difference in survey scale has an effect on the average measures of structural complexity as mentioned above. Because coral colonies intrinsically shape reef structure [94], the relationship between structural complexity and coral cover is reciprocal, where coral species composition influences habitat structure and vice versa [8,51]. Several studies have documented the positive relationship between complexity metrics and coral cover [8,15,49,95], lending further support to the results reported in this study.

Considering the importance of survey scale when examining the relationship between coral (and other organisms) and reef structure [15,51,96–98], the measurements of structural complexity across multiple spatial scales provide more insight into the topographic complexity of benthic communities and habitats on reefs [40]. In addition to the spatial scale, the sizes and growth forms of benthic organisms, as well as the substrate and habitat type, can significantly contribute to the structural complexity of reefs. The colony size and growth morphology of corals have been found to be significant determinants of reef complexity in Guam [93] and elsewhere [11,99], which can also explain the predominantly positive correlation between coral cover and slope observed in this study. The majority of corals on the reefs in this study formed large colonies with columnar, branching, or massive morphologies, all of which have been shown to significantly contribute to structural complexity [11,93,99]. This also explains the primarily positive correlation observed between coral cover and VRM, as the 5 cm resolution is best suited to quantify the roughness of corals with massive, tabular, or other large morphologies [39,99]. However, the VRM is significantly impacted by scale, where smaller resolutions (1 cm) have been shown to best quantify the roughness of rubble, branching and encrusting coral, and crustose calcifying red algae [39,99,100]. While these studies primarily focused on corals, the diverse morphologies and size ranges of other significant contributors to reef communities, such as macroalgae and sponges [101,102], would also likely influence the structural complexity of reefs. This emphasizes the importance of comprehensive benthic surveys across taxonomic groups in combination with structural complexity metrics to develop a holistic approach to reef health assessments.

This study is among the first to characterize the 3D structure of coral reef communities in Guam using SfM photogrammetry. This baseline allowed for a comparison of the structural complexity of Guam's reefs with reefs from elsewhere in the world. Considering the suite of ecological descriptors that are influenced by structural complexity, the inclusion of such metrics could augment future monitoring efforts. The analyses revealed significant relationships between terrain complexity metrics and benthic diversity or, more crucially, coral cover. Declining reef health poses substantial cultural, economic, and ecological concerns worldwide. The drastic decline in reef structural complexity due to the degradation of reef habitats and the loss of coral cover can severely impact a number of ecosystem processes (e.g., biodiversity, disturbance recovery, resistance to climate change, and coastal protection) [14–19]. As such, quantifying the structural complexity of reefs can prove instrumental when making conservation and management decisions. While recognizing that expanding the range of depths and spatial scales surveyed may provide a more complete topographic characterization of reefs, this study demonstrates that fast, effective, and repeatable surveys are feasible at ecologically relevant scales. In evaluating the relationship between declining reef health and reduced structural complexity [54], rapid structural complexity surveys can benefit reef conservation and monitoring efforts.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/rs15235558/s1, Figure S1: General linear models showing significant relationships between benthic diversity and structural complexity metrics ($p < 0.05$) modeled irrespective of site; Figure S2: General linear models showing significant relationships between coral cover and structural complexity metrics ($p < 0.05$) modeled irrespective of site; Table S1: Table that contains all metrics that were calculated and analyzed as part of this study, as well as the start and end coordinates in decimal degrees (DDs) of each transect; Table S2: Table of photoquadrat point counts of 67 consolidated benthic groups used to calculate Shannon Diversity Index (H) and scleractinian coral cover for each transect/site; Table S3: List of benthic categories used to analyze diversity, including the scleractinian coral species used when estimating coral cover.

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Data Availability Statement: The data computed and analyzed in this study are summarized in Table S1. However, the spatial datasets (DSMs) generated and/or analyzed during this study are available from the corresponding author upon reasonable request. These data are not publicly available due to the substantial file sizes.

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