



# A Protocol for Extracting Structural Metrics From 3D Reconstructions of Corals

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The 3D structure of individual coral colonies provides insights into their ecological functioning. While structure from motion techniques make it possible to reconstruct 3D models of coral colonies based on overlapping images, the extraction of relevant metrics of complexity in a reproducible way remains challenging. We present a method and associated scripts for the 3D reconstruction of coral colonies from *in-situ* images and the automatic extraction of eleven structural complexity metrics, designed to be run in widely-used software packages. The metrics are designed to capture aspects of complexity relating to the colony's size and shape that are related to their ecological function. We explored the potential ecological applications of some of these metrics using linear models, comparing aspects of complexity among colonies of different size and morphotaxa (combined information on morphology and taxa). Our results showed that a metric as simple as colony diameter explained 95% of the variation in shelter provisioning capability when paired with information on colony morphotaxa. Further, the habitat provisioning of colonies of comparable size was similar among the six of the seven morphotaxa examined. During the current period of rapid uptake of photogrammetry among ecologists, the results of our study provide a basis to use data derived from 3D models to further explore the nuances of the relationship between structure and function of corals at the colony scale in a replicable and standardised way.

**Keywords:** photogrammetry, structural complexity, spatial refuge, automation, structure-from-motion

## INTRODUCTION

Structural complexity is an important component in the functioning of ecosystems, with the abundance and diversity of species generally being positively related to structural complexity of the habitat, especially at low levels of complexity (MacArthur, 1958). The presence of structure creates protected environments that moderate environmental conditions and creates a wide breadth of

ecological niches for animals to exploit (Bruno et al., 2003; Alvarez-Filip et al., 2011; Tokeshi and Arakaki, 2012). As the abundance and diversity of complex physical structures in an ecosystem increases, so does the ability of that ecosystem to support animals with different microhabitat needs (Willis et al., 2005). Whilst the effects of structural complexity are often confounded by differences in the taxonomic composition of habitat-forming organisms, its importance transcends any particular ecosystem and is applicable in almost every natural habitat, from terrestrial coniferous forests (Franklin and Van Pelt, 2004) and savannahs (Gigliotti et al., 2020) to freshwater rivers (Warfe and Barmuta, 2006) and coral reefs (Graham and Nash, 2013).

On coral reefs, one of the world's most biodiverse ecosystems, the importance of structural complexity has long been recognized (Risk, 1972; Vine, 1974). The availability of complex structure provides refugia from predators (Ménard et al., 2012; Rogers et al., 2014; González-Rivero et al., 2017), reduces competition for habitat space through the formation of diverse and abundant ecological niches or microhabitats (Graham and Nash, 2013) and increases the surface area available for foraging (Vine, 1974). Whilst the abundance, density and spatial arrangement of habitat-providing structures are important in shaping fish communities (Pygas et al., 2020), the structural characteristics of individual coral colonies can also play an important role for many small-bodied, site-attached fishes (Quadros et al., 2019). For example, structurally complex colonies are good providers of habitat because they generally supply a large amount of physical refugia from larger bodied predators (Hixon and Beets, 1993; Noonan et al., 2012). As such, fish-habitat relationships vary according to the species of coral and fish, and also change over time according to colony growth and/or erosion (Graham and Nash, 2013; Ferrari et al., 2017). The physical structure provided by individual coral colonies has been related to differences among coral species and/or growth forms (Komyakova et al., 2013; Richardson et al., 2017; Urbina-barreto et al., 2020), among colony sizes (Noonan et al., 2012; Agudo-Adriani et al., 2016; Urbina-barreto et al., 2020), and with environmental setting (Todd, 2008; Ow and Todd, 2010; Dospot et al., 2019). Despite the importance of the structural complexity of coral colonies, accurately quantifying the physical structure of individual colonies is challenging.

At the scale of individual coral colonies, technical limitations have led to simplified measurements of structural complexity, including the manual measurement of the space between colony branches (Noonan et al., 2012), measurements of colony morphometrics such as height and diameter (Harborne et al., 2011; Harborne et al., 2012), as well as estimates of surface area from foil-wrapping or wax-dipping branches (Veal et al., 2010). However, these methods are generally imprecise, cannot be easily repeated *in situ*, and often damage the colonies (Naumann et al., 2009; Ferrari et al., 2016). Recent advances in computer vision and processing have allowed the full dimensionality of objects to be recorded and analyzed through 3D reconstructions of high-resolution imagery (i.e., close-range photogrammetry; Lavy et al.,

2015; Bayley and Mogg, 2020), which is becoming popular among ecologists.

Underwater close-range photogrammetry offers enormous potential to investigate the physical structure of coral colonies, however there is a need to explore and develop new, ecologically relevant metrics that can be compared among and within coral taxa. The process of analyzing reconstructed objects is now readily accessible and the structure of coral colonies can be analyzed in numerous ways (Figueira et al., 2015; Ferrari et al., 2016). Several metrics offer valuable insights into the structure of colonies including 3D surface area, colony volume, and a variety of ratios, including surface area to volume ratio, and colony rugosity (a ratio of the 3D to 2D surface area) (Bythell et al., 2001; Agudo-Adriani et al., 2016; Ferrari et al., 2016; Dospot et al., 2019; Zawada et al., 2019a). However, metrics that focus on the delivery of an ecological function, such as shelter provisioning, are somewhat rare (but see Madin et al., 2016; Urbina-barreto et al., 2020). Given the rapidly changing ecological composition of global reef communities due to the combined effects of climate change (Hughes et al., 2017b; Hughes et al., 2018; Richardson et al., 2018; Dietzel et al., 2021) and local anthropogenic stressors (Cheal et al., 2017; Suchley and Alvarez-Filip, 2018), metrics that reflect the ecological functions of corals are required (Madin et al., 2016; Dospot et al., 2019; Streit et al., 2019). Progress has been made to this end recently, as ecologists are exploring the structural traits of coral colonies in more detail. Quantification of the shelter provisioning capability and size structure of available refuge spaces have been discussed in specific types of coral (Urbina-barreto et al., 2020), as well as how this metric changes over time with coral growth (Million et al., 2021). Underwater close-range photogrammetric reconstructions have also revealed complex, non-linear relationships between simple coral growth measurements, such as linear extension rates, and higher order traits, such as shelter provisioning (Million et al., 2021).

Several aspects of the process of underwater photogrammetry have been assessed to date, including the effects of various parameters such as photograph density and resolution (Marre et al., 2019), camera systems (Guo et al., 2016), lenses and housings (Menna et al., 2016), water turbidity (Bryson et al., 2017) and flying elevation (Marre et al., 2019). Whilst it is of critical importance to understand how models may be affected by user-decisions, comparability between studies could and should be improved by the adoption of standardised workflow procedures. Given that there exist multiple studies based on photogrammetry and deriving estimates of complexity from corals (Agudo-Adriani et al., 2016; Reichert et al., 2016; Dospot et al., 2019; Vivian et al., 2019; Million et al., 2021), there is great incentive to adopt reproducible methods *via* the use of standardised workflows at key parts in the processing pipeline. This applies both to the reconstruction of coral models (Lange and Perry, 2020) and the extraction of structural complexity metrics.

The aim of this study is to ensure repeatability among users by using a python script to serially process 3D reconstructions of coral colonies and extract a suite of three-dimensional complexity metrics. Following manual isolation of colonies from the

surrounding benthos in the models, we developed a second python script that automatically extracts a suite of three-dimensional structural complexity metrics from each model, saving time and increasing repeatability among users. To investigate the utility of these metrics as ecological indicators, we compared two of these key metrics among 69 colonies of varying size and morphotaxa using Bayesian linear regression models.

## METHODS

### Data Collection and Classification of Corals

Images of 69 colonies were collected from seven reefs on the Great Barrier Reef (GBR) and in the Coral Sea during February 2020 (GBR: Hickson, and Tiger Reefs; Coral Sea: Saumarez, Cato, Wreck, Frederick, and Marion Reefs). The imaged colonies were located at depths between 3 to 13m in sheltered, back reef environments on each reef. Colonies with partial mortality, disease or algal overgrowth were avoided, as this may have affected structural characteristics.

Given the difficulties in identifying coral colonies to species in the field, we used morphotaxa to allow relevant comparisons. Individual colonies from each of the following seven morphotaxa were haphazardly selected and imaged: corymbose *Acropora*, digitate *Acropora*, tabular *Acropora*, branching *Isopora*, branching *Pocillopora*, branching *Porites* and ‘massive’ corals (**Figure 1**). Massive and submassive corals from different genera (mainly *Porites* and *Favia*) were aggregated into a single category (i.e., ‘massive’ corals) due to their structurally comparable morphologies and because none of the massive coral colonies imaged had overhangs contributing to their refuge space. To classify coral morphology, we followed the CATAMI scheme (Althaus et al., 2015), which includes visual guides to broad-level morphologies.

### Field and Laboratory Equipment

Camera system choice has been shown to play an important role in the quality of the final model (Marre et al., 2019). Resultant models from different camera/computer systems can be of comparable quality, however these should always be reported since the resolution (i.e., the smallest resolvable details) can be affected. All images used in this study were taken using a Canon 5D MK IV body (Canon USA Inc.) Ikelite housing (Ikelite Underwater Systems), fitted with an 8” dry lock dome port. A Canon 35mm f/2 IS USM prime lens was used to minimize perspective distortion in photographs while a dome port was chosen to reduce barrel distortion near the edges of images (Menna et al., 2018). Each photograph was a 30.2 Megapixel JPEG image. Relevant PC system specifications were as follows: Intel Core i9 9900K 3.6GHz CPU, 64GB RAM, 1x NVIDIA GeForce RTX 2080Ti Graphics card. High resolution 3D models are possible using cheaper, more compact cameras and off-the-shelf laptops (Lange and Perry, 2020). However, changes in model resolution and processing times associated with different cameras and processing settings affect surface measurements and

may hinder comparisons if not given appropriate consideration. At the colony scale, flying elevation is low (i.e., the sensor is very close to the object of interest), so sufficient overlap is likely to result in comparable model qualities regardless of sensor size (see Menna et al., 2016; Marre et al., 2019 for discussions of camera systems and flying elevation).

Agisoft recommends the use of coded targets for model scaling purposes. We mounted these in pairs (12-bit, printed on waterproof paper) on to two galvanized steel bars at known measured distances apart, ready for automatic detection by the software.

### Data Collection Protocols

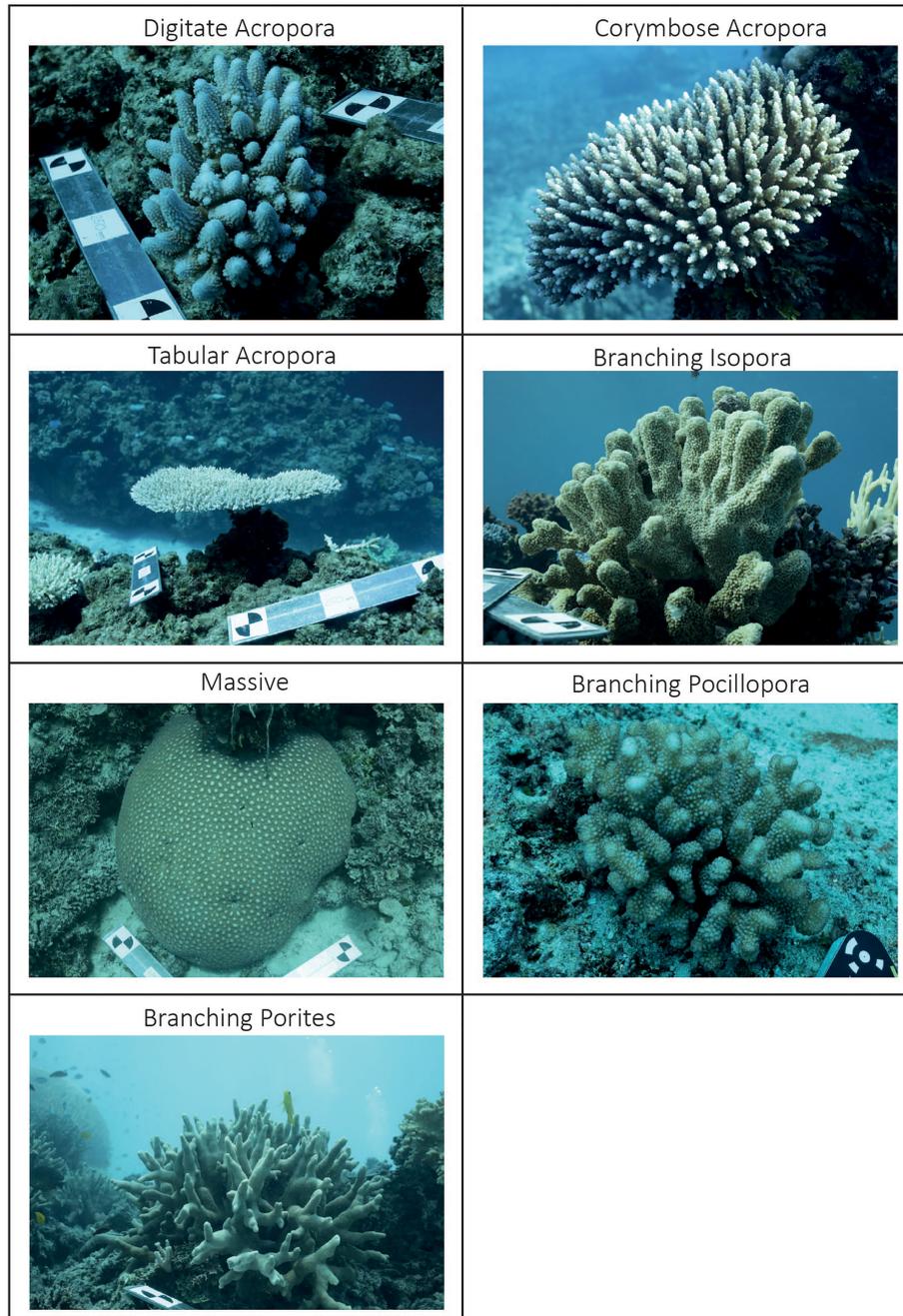
The two scale bars were first placed adjacent to the coral colony prior to taking images and were included in a minimum of 20 photographs per colony. For each colony, 100-250 images (depending on colony size and morphotaxa) were taken. The goal was to collect a set of overlapping images taken from multiple angles such that the entire colony was imaged (Bythell et al., 2001; Million et al., 2021). We used an orbital swimming motion – three to four 360 degree passes around the colony at different heights. Imaging for a colony generally took 3-5 minutes (based on 100-250 images plus time before for testing camera settings). It is not critical that swimming motion is identical to generate comparable data, only that the entire colony is imaged with sufficient overlap to resolve all required details in the resultant model.

Camera settings were chosen based on local light conditions, but aperture was fixed at f/10 to ensure the entire colony was in focus during imaging.

### Model Reconstructions and Extraction of Structural Complexity Metrics

A variety of paid and free options are available to generate structure from motion models. The choice of software has been shown to lead to differences in the measured characteristics, affecting repeatability and potentially comparability between model data from different studies (Forsmoo et al., 2019). Agisoft Metashape (formerly Photoscan) is the most popular choice of software among ecologists for generating coral reconstructions (Agisoft LLC, St. Petersburg, Russia). 3D models were constructed using Agisoft Metashape Professional Ver 1.7. Total processing time for models varied; massive morphologies with ~150 images per colony took approximately 10-20 minutes to process, whereas larger and complex colonies with image sets numbering over 200 required several hours of processing. Steps for model generation have been discussed extensively, including error reduction, photograph selection, model scaling and accuracy metrics (Green et al., 2014; Forsmoo et al., 2019; Lange and Perry, 2020).

A single python script to reconstruct colonies using the same processing workflow is available (<https://github.com/E-Aston/CoralGeometry>). This script comes with detailed instructions and is interactive within Metashape, designed to be run from within the graphical user interface using the “Run Script” command. These instructions are also provided as **Supplementary Material**. For the use of this script, no



**FIGURE 1** | *In situ* examples of the seven distinct modelled morphotaxa. Note the galvanised scale bars present in several panels used to scale the reconstructions.

knowledge or installation of python is required, only installation of Metashape Professional. On execution of the script, a series of dialogue boxes prompt users to input the settings to be used in serial processing of the models, including the quality threshold for the disabling of photographs, photo alignment accuracy, and dense cloud quality. We provide the settings used to reconstruct the colonies used in this study (**Table 1**), and strongly recommend that others use the same settings when following this

reconstruction protocol, since processing settings affect model resolution and thus final measured characteristics.

Following the reconstruction of models, some manual preparation is needed for metrics extraction. Given the *in-situ* nature of our data collection, some of the benthos to which corals are attached is also reconstructed and needs to be removed manually. This includes “isolating”, i.e., removing any benthos from the reconstruction using metashape such

**TABLE 1** | Beginning to end of reconstruction pipeline in Metashape.

Workflow Step	Details
1. Remove low-quality images (A)	Disable photos with quality score <0.5
2. Detect markers (A)	Tolerance value is set to 30 by default
3. Align Photos (A)	High Accuracy, generic preselection, Key Point Limit: 40,000 Tie Point Limit: 4,000
4. Clean Sparse cloud and optimize cameras (A)	Three-step automatic iterative process to remove the worst tie points based on reprojection error, reconstruction uncertainty and projection accuracy. Recommended setting: 95 (removes the worst 5% of points at each step in the process).
5. Build Dense Cloud (A)	Quality: Medium Depth filtering: Mild Calculate point colors
6. Build Mesh (A)	Source data: Dense cloud Surface type: Arbitrary (3D) Face count: High Interpolation: Enabled Calculate vertex colors: Yes
7. Build Texture (A)	Mapping mode: Generic Blending mode: Mosaic Texture size/count: 4096 x 1 Enable hole filling: Yes Enable ghosting filter: yes
8. Isolate model (M)	Free-form selection tool Select and delete all faces in the model that are not part of the reconstructed colony
9. Model scaling (M)	Manually delete incorrectly detected markers. Enter distance between targets in reference pane. Update model to apply scaling
10. Object orientation (M)	Use the navigator tool to manipulate the colony to a top-down view (perpendicular to the orientation of upwards growth). Generate report for model with projection set to 'current view'. Planar area is found as 'coverage area' on page 2 of the.pdf which will automatically open on generation. Metric is given in m <sup>2</sup>
11. Export object	Export each completed isolated mesh to a single folder in preparation for metrics extraction

*These settings were the same for each model in the dataset. Within the workflow steps, (M) refers to manual steps needed to be performed by the user, (A) refers to steps automated using the python script.*

that they are ready for automatic metric extraction (**Table 1**). The only measure of colony geometry to be extracted from metashape is planar area, which is automatically calculated using a top-down view upon generation of the model report (**Table 1**; Step 9).

## Extraction of Structural Complexity Metrics

Ten further metrics of the surface geometry or structural complexity were extracted from each colony, using a custom-coded python script utilizing the package *pymeshlab* (Muntoni and Cignoni, 2021), which integrates with the open source 3D software MeshLab v2016.12 (Cignoni et al., 2008). This package contains the full capability of MeshLab without the need to manually obtain surface measurements for each mesh. Our script 'cleans' the mesh (i.e., removes any unwanted faces that are not attached to the colony itself, which are often still present following the export of the model), then applies a series of scripts to measure and calculate several geometric complexity metrics automatically. These higher order complexity metrics were: 3D surface area, colony volume, convex hull volume (the simplest polygon that fully encloses the colony), absolute spatial refuge (a volumetric measurement of the space generated by the interstices of each colony), surface area to volume ratio, shelter size factor (fragmentation of shelter volume), proportion occupied (the ratio of the convex hull volume occupied by the colony), colony maximum diameter and colony height. A detailed summary of these metrics is presented below as well

as how each is calculated (**Table 2**), in addition to a graphical representation of metrics (**Figure S1**).

Given a set of reconstructions in the form of .obj files (the standard output from Metashape), the code returns a .csv file populated with the value of each metric for every coral, saving up to several hours of manual calculations. The use of the metrics extraction script assumes zero knowledge of python programming on the part of the user. All that is required is installation of python and the ability to run scripts from an interpreter. We provide detailed instructions on how to do this in **Supplementary Material**. For further analysis, we investigated a small subset of these (diameter, absolute spatial refuge and shelter size factor), however depending on the research questions, any of the described metrics are extracted and available for analysis.

## Statistical Models for Methods Validation

To assess the validity of the calculated complexity metrics extracted using our python script we selected two of the higher order and popularly used metrics and compared them among colonies of different size and morphotaxa. We chose absolute spatial refuge and shelter size factor. Although any of the 3D metrics presented in this study may be ecologically informative depending on the research question, quantifying the shelter capacity of corals and how this shelter is delivered (i.e. the fragmentation of the shelter) is broadly applicable for ecological purposes, including measuring the functional capacity of corals to provide habitat (Urbina-barreto et al.,

**TABLE 2** | Summary of metrics calculated for each colony using a combination of Metashape and MeshLab.

Metric name	Description	Unit	Software	Ecological reasoning/application
Colony diameter ( $D$ )	Length along X axis of bounding box (the longest horizontal axis) enclosing each colony	cm	Python/ Meshlab	Widely used in the literature as a basic size metric. Also used to relate to higher order complexity metrics (House et al., 2018; Urbina-barreto et al., 2020)
Height ( $H$ )	Length along Z-axis of bounding box enclosing each colony	cm	Python/ Meshlab	Identified as important for fish abundance (Harborne et al., 2011; Harborne et al., 2012; Agudo-Adriani et al., 2016)
Planar area ( $A_{2D}$ )	Total area of reef floor occupied by each colony	cm <sup>2</sup>	Metashape	Important metric of spatial occupancy of the reef floor by each colony. Used to calculate popular metrics such as percent cover and useful for examining how different colonies fit together within a patch of reef. Also useful for growth rates (Ferrari et al., 2016; Dornelas et al., 2017)
3D Surface area ( $A_{3D}$ )	Total surface area of colony	cm <sup>2</sup>	Python/ Meshlab	Relevant metric of potential foraging area provided to corallivores (González-Rivero et al., 2017). Also related to metabolic processes in corals such as photosynthesis (Naumann et al., 2009) Also used to measure 3D growth of colonies (Ferrari et al., 2017a)
Volume ( $V$ )	Total volume of colony	dm <sup>3</sup> (litres)	Python/ Meshlab	Metric related to biomass, size and carbonate production. Also used over time to infer growth rates (Lavy et al., 2015; House et al., 2018)
Convex hull volume ( $V_{CH}$ )	Volume of the simplest polygon which fully encloses the coral	dm <sup>3</sup> (litres)	Python/ MeshLab	Intermediary step for calculating other metrics related to interstitial space generated by colonies (Dospot et al., 2019; Urbina-barreto et al., 2020).
Absolute spatial refuge ( $R$ )	Volume of the total amount of space generated by each coral ( $R = V_{CH} - V$ )	dm <sup>3</sup> (litres)	Python/ Meshlab	Quantifies interstitial space, with potentially important links to inhabitant fish (Urbina-barreto et al., 2020). Can potentially be used over time to track coral growth in an ecologically relevant manner (Million et al., 2021). Higher values of $R$ indicate more overall shelter volume. This metric is calculated by subtracting the volume of the colony itself from the volume of its enclosing convex hull, leaving a volumetric measure of the interstitial space generated by each colony.
Surface area to volume ratio	Ratio between 3D surface area of a colony to its volume ratio ( $A_{3D} \div V$ )	Ratio	Python/ Meshlab	Ecologically important metric of colony surface complexity that can be used to compare corals of different morphology (Dospot et al., 2019). Higher surface area to volume ratios indicate greater surface complexity.
Shelter size factor ( $S$ )	Ratio of Absolute spatial refuge ( $R$ ) to 3D surface area ( $S = R \div A_{3D}$ )	Ratio	Python/ Meshlab	Quantifies the level of fragmentation of habitat space, useful for comparing the size structure of refugia among colonies of different size and morphology (Urbina-barreto et al., 2020). Higher values indicate comparatively more "open" structures and larger spaces due to the higher volume of shelter space relative to colony surface area.
Proportion occupied ( $ProCC$ )	Ratio of colony volume to convex hull volume ( $ProCC = V \div V_{CH}$ )	Ratio	Python/ Meshlab	Quantifies compactness, a particularly useful metric for branching colonies (Dospot et al., 2019). A higher proportion occupied indicates a more compact branching structure. Also referred to as convexity (Zawada et al., 2019a).

A graphical representation of metrics is available in **Figure S1**.

2020) and tracking how this changes over time with colony growth (Million et al., 2021). We hypothesized that due to differences in the physical structure of colonies of different morphotaxa, the rate of increase in absolute spatial refuge volume with colony size would vary among morphotaxa. We also hypothesized that the differences in physical structure would result in variation in the size-structure of spatial refuges among colonies of different size, again with parameters specific to each morphotaxa considered.

To determine whether 3D metrics of complexity (in this case spatial refuge) could be predicted by simpler linear metrics (i.e., colony diameter) we fitted two Bayesian linear regression models using the package 'brms' (Bürkner, 2017), both using colony diameter to predict the value of a 3D complexity metric. The first was absolute spatial refuge and the second was shelter size factor. For each of these models, morphotaxa was included as a predictor, so we could also infer how the scaling relationships between these variables differed among morphotaxa.

Appropriately informative Gaussian priors were used to inform the model and restrict to a reasonable outcome space (Banner et al., 2020). Assumptions about the underlying data distribution and prior predictive distributions were chosen based on visual exploration of the data following transformations as well as previous studies that have used similar data in the same way (Urbina-Barreto et al., 2020). Priors for all models were assessed visually using randomly sampled lines from the prior probability distribution (**Figure S2**). Posterior distributions were obtained using four Markov Chain Monte Carlo (MCMC), with 20,000 iterations and a warmup period of 10,000 samples. Inferences about the strength of the relationships between variables in both models were based on 95% highest density probability intervals around means predicted from the posterior distribution of the models. Analyses were carried out using R 4.0.1 (<https://r-project.org>). Initial data exploration of 2D and 3D variables was carried out using a scatterplot matrix on raw data generated using the 'Ggally' package (**Figure S2**) (Schloerke et al., 2020,

<https://cran.r-project.org/package=GGally>). Plotting was carried out using the package *ggplot2* (Wickham, 2015). Bayesian  $R^2$  values were obtained to assess how well the regression models fitted the data in each case.

### Model 1: Absolute Spatial Refuge (R) vs. Diameter (D)

Prior predictive distributions were set using the results of regression models previously fit to this data type (Urbina-Barreto et al., 2020). Our data encompassed a similar size range of colonies; the main difference was that we chose to classify based on morphotaxa, a combination of taxonomic identity (genus) and morphology, rather than just morphology. We used log colony diameter  $Dlog_i$  and an indicator variable for morphotaxa (colony ID = CID) to predict log absolute spatial refuge for each colony  $Rlog_i$ , with the following model structure:

$$Rlog_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha_{CID[i]} + \beta_{CID[i]} Dlog_i$$

$$\alpha_{CID} = \text{Normal}(-9, 0.5)$$

$$\beta_{CID} = \text{Normal}(3, 0.5)$$

$$\sigma = \text{Exponential}(1)$$

We assumed a normal distribution with mean  $\mu_i$  and standard deviation  $\sigma$ . The prior values for the intercept  $\alpha$  was the same for each morphotaxa, as was the slope value  $\beta$ , reflective of Urbina-Barreto et al. (2020). An intercept of -9 on the log scale is close to 0 on the natural scale, so scientifically this prior made sense. This subverted the need to attach uninformative priors to the slope and intercept values or to rescale the data in a way that would result in a loss of information in the posterior distribution. These priors were relaxed enough to allow data to drive any differences in the posterior predictions between morphotaxa. An exponential prior with mean 1 was assigned to the standard deviation  $\sigma$ , given that we knew little about this parameter beforehand.

This model was compared to one without the morphotaxa variable using pareto-smoothed importance sampling leave-one-out (PSIS-LOO), to determine whether splitting

colonies into morphotaxa resulted in an improved fit to the data (Yao et al., 2018).

### Model 2: Shelter Size Factor (S) vs. Diameter (D)

Because shelter size factor is a new metric, we used less informative priors to allow the data to drive the model fit. We used colony diameter to predict shelter size factor for each morphotaxa. The model structure was:

$$S_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha_{CID[i]} + \beta_{CID[i]} D_i$$

$$\alpha_{CID} = \text{Normal}(0, 0.5)$$

$$\beta_{CID} = \text{Normal}(4, 2)$$

$$\sigma = \text{Exponential}(1)$$

Where  $S_i$  is the shelter size factor of each colony  $i$ , normally distributed with mean  $\mu_i$  and standard deviation  $\sigma$ .  $D_i$  is the diameter of each colony  $i$ , and this model. The morphotaxa indicator CID was the same as the previous model. Since shelter size factor is dimensionless, we did not log-transform any of the variables for this model. The same exponential prior was assigned to the standard deviation  $\sigma$  as in the previous regression model. To see whether morphotaxa and colony diameter were useful predictors of shelter size factor, and to check for overfitting, models with and without morphotype were compared, again using PSIS-LOO (Yao et al., 2018).

## RESULTS OF STATISTICAL MODELS

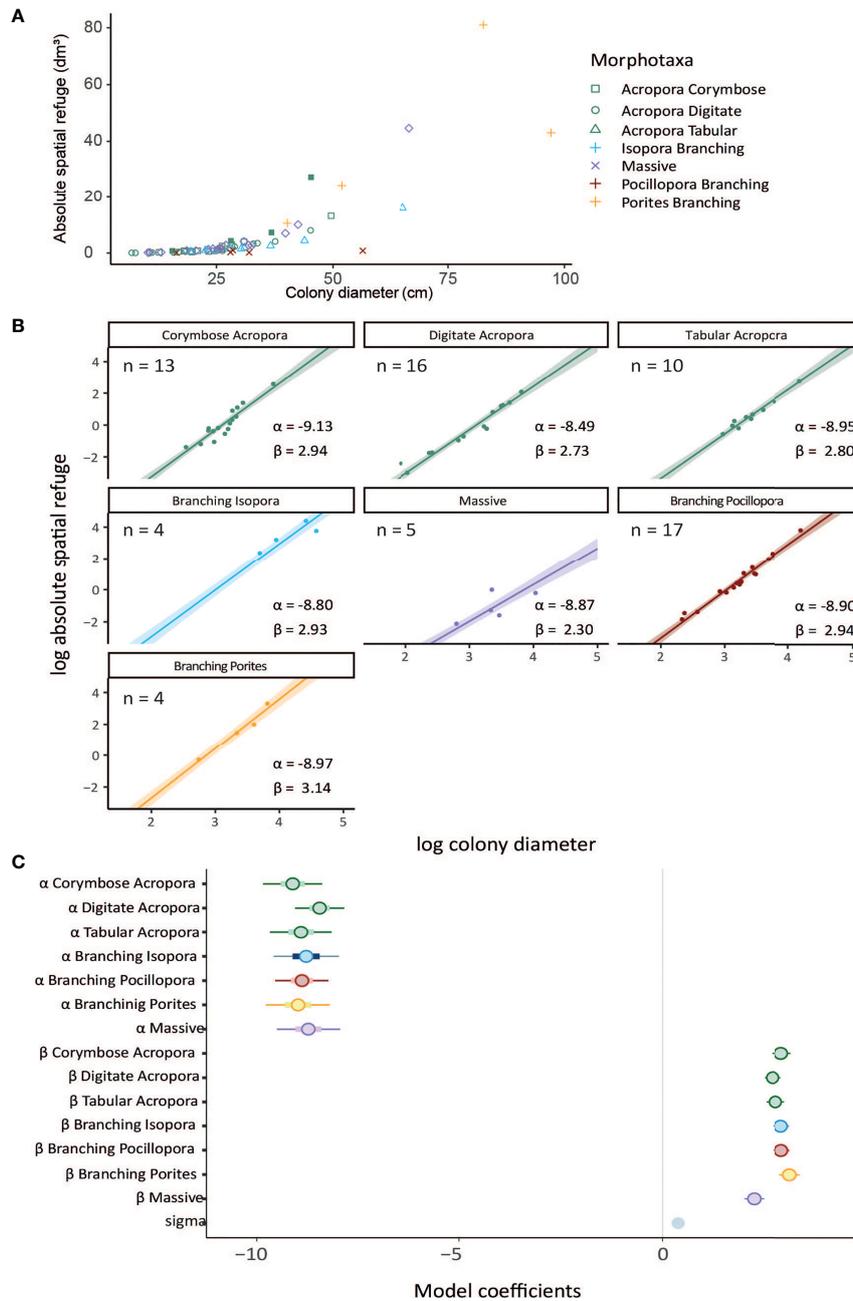
Sixty-nine colonies across the seven morphotaxa (range: 4-17 colonies per morphotaxa) were used for morphometric analysis (Table 3). Colonies ranged in diameter from 6.8 to 97.1 cm [mean diameter:  $29.6 \pm 2.0$ cm (s.e)] though size distribution was skewed towards smaller colony sizes with 44 of the 69 colonies being < 30cm in diameter. Measurement error was very low across the dataset, with a maximum scaling error of 0.5mm across the entire sample. Most were considerably lower and fell in the range of 0.1-0.3mm scaling error.

**TABLE 3 |** Summary of representation and dimensions among the seven unique morphotaxa used for colony reconstructions.

Morphotaxa	<i>n</i>	Mean Diameter ( <i>D</i> ) (cm ± se)	Mean Absolute spatial refuge ( <i>R</i> ) (dm <sup>3</sup> ± se)	Mean Shelter size factor ( <i>S</i> ) (± se)
Branching Pocillopora	17	27.6 ± 3.2	4.923 ± 2.559	0.85 ± 0.11
Digitate Acropora	16	24.2 ± 2.1	2.0129 ± 0.794	0.80 ± 0.08
Corymbose Acropora	13	23.2 ± 3.4	1.8682 ± 0.653	0.67 ± 0.09
Tabular Acropora	10	32.5 ± 4.3	3.1685 ± 1.470	0.95 ± 0.16
Massive	5	32.3 ± 6.6	0.4842 ± 0.177	0.21 ± 0.06
Branching Isopora	4	68.0 ± 13.2	39.758 ± 15.271	3.96 ± 0.69
Branching Porites	4	31.4 ± 6.4	9.940 ± 5.955	2.31 ± 0.06

Note that these are summary statistics only and were not tested statistically for between-group differences.

Shelter size factor is a ratio of the overall spatial refugia volume to the 3D surface area of the colony and is thus unitless. Units for absolute spatial refuge are given in cubic decimetres. One cubic decimetre is equivalent to one litre.



**FIGURE 2 | (A)** Scaling of absolute spatial refuge with increasing colony diameter across all morphotaxa. **(B)** Plotted posteriors from log-log linear model of absolute spatial refuge (mean centred) from the interaction model containing colony diameter as a predictor for each of the seven coral morphotaxa as well as intercept ( $\alpha$ ) and slope ( $\beta$ ) estimates. Shaded regions are 95% highest density probability distribution. **(C)** Posterior predictions for intercept  $\alpha$  and  $\beta$  parameters in the model. Straight line slope parameters indicate the existence of power-law relationships, with steeper slopes corresponding to higher power-scaling. Points indicate means, thick bars are 50% credible intervals, thin blue lines are 95% credible intervals. Numerical values of all model coefficients including posterior uncertainty are included in **Table S1**.

### Model 1 Predictions: Log-Absolute Spatial Refuge (R) vs. Log-Diameter (D)

The best model for predicting absolute spatial refuge included the interaction between morphotaxa and colony diameter (PSIS-LOO model weighting = 1, Bayes  $R^2 = 0.95$ ) (**Table S2**). Most

morphotaxa appeared to fall within a somewhat similar range of increasing spatial refuge with increasing colony diameter (**Figures 2A, C** and **Table S1**). For most morphotaxa, posterior credible intervals were narrow and most colonies fell near the mean prediction slope (**Figure 2B**). The linear model

determined that the scaling of absolute spatial refuge with colony diameter was broadly similar among almost most of the morphotaxa included in this study (95% credible intervals for the posterior estimates of slope overlapped between morphotaxa in most cases, **Table S2**), but there were some differences in the scaling relationships among morphotaxa. The exception was ‘massive’ corals, where the increase in spatial refuge was considerably lower than the six other morphotaxa with increasing colony diameter.

The relationships in the models indicate that there is a power-law relationship between colony diameter and spatial refuge provisioning such that as colonies grow and increase in size, the rate of increase of spatial refuge rises exponentially. Thus, subtle differences in slope gradients on the log-scale become larger when converted back to the natural scale, particularly in larger colonies (**Figure 2A**). For example, absolute spatial refuge in digitate and corymbose *Acropora* scaled to the power of 2.73 and 2.94 respectively (maximum likelihood estimate). For a colony of diameter 25cm, the expected spatial refuge volume would be 1.34 and 1.39dm<sup>3</sup> (1dm<sup>3</sup> = 1000cm<sup>3</sup> or 1 litre) for digitate and corymbose *Acropora* respectively. Following the same scaling law, by the time colonies reach a diameter of 50cm, the expected values of refuge volume would be approximately 8.85dm<sup>3</sup> and 10.59dm<sup>3</sup>, a difference of approximately 20%. For large colonies of diameter 75cm for example, a digitate *Acropora* colony would provide an estimated 27 dm<sup>3</sup> (27 litres equivalent) whilst a comparable corymbose *Acropora* colony would provide an estimated 35.5 dm<sup>3</sup>, a comparatively large difference (36% larger). By contrast, at this large colony size, a branching *Pocillopora* colony, which was also captured well in this study, would have an expected absolute spatial refuge of 44.7dm<sup>3</sup>, scaling at a greater rate with increasing diameter than any of the *Acropora* morphotaxa.

For ‘massive’ colonies, the increase in spatial refuge with increasing colony diameter was the lowest, this group consistently providing the lowest volumes of absolute spatial refuge. A colony with diameter 50cm would have an expected spatial refuge of just 1.13dm<sup>3</sup>, or just over 1.1 litres. Whilst there was relatively little data for this morphotaxa, massive corals clearly provide the least spatial refuge among all morphologies considered in this study.

## Model 2 Predictions: Shelter Size Factor (S) vs. Diameter (D)

The best model was again the interaction model containing morphotaxa (PSIS-LOO model weighting = 1, Bayes  $R^2 = 0.84$ ) (**Table S4**). Whilst shelter size factor was predicted well by the combination of colony diameter and morphotaxa, (branching *Acropora*, *Pocillopora*, digitate *Acropora* and tabular *Acropora*, there were no strong differences in the rate of increase of shelter size factor with increasing colony diameter in the posterior predictive distributions (**Figure 3** and **Table S3**), with the rate of increase estimates ( $\beta$ ) overlapping in all cases. For all morphotaxa except ‘Massive’ corals, shelter size factor ( $S$ ) and colony diameter ( $D$ ) were positively correlated (**Figure 3**). ‘Massive’ corals had the lowest values of shelter size factor across all colony sizes and a very small increase in shelter size factor with colony diameter. For branching *Isopora* and *Porites*, which respectively had high values

for  $\alpha$  and  $\beta$ , we could not make and valid statistical inferences since the sample sizes were too low.

## DISCUSSION

### Metrics Extraction From Reconstructed 3D Models

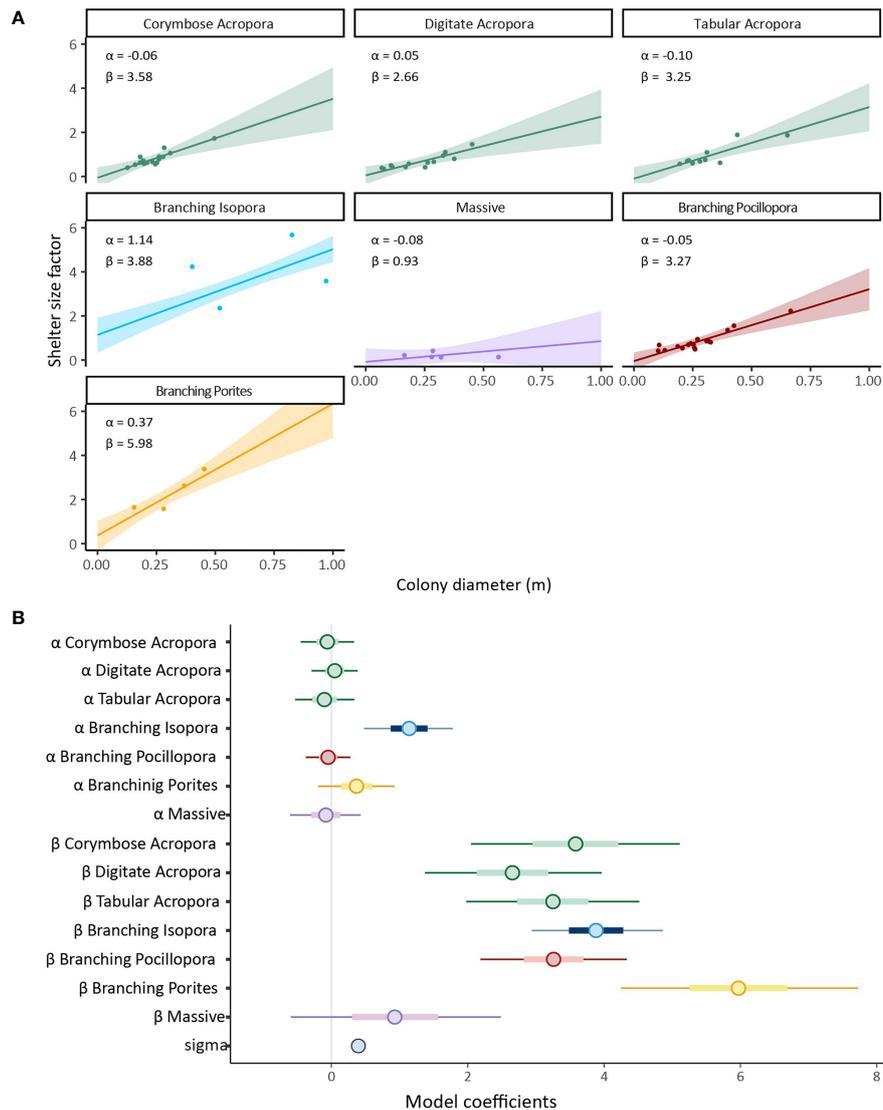
The methods developed in this study allow for the automated extraction of a suite of informative structural complexity metrics from digital reconstructions of coral colonies (or other objects). Applying novel technologies to create 3D reconstructions is accessible, accurate and requires little training. Yet, there is limited guidance on how to apply these technologies for ecological studies. Much of the recent literature deals with the accuracy, precision and repeatability of the resultant models, as well as how to make the reconstructions themselves, laying a critical foundation for the broad uptake of this method (Figueira et al., 2015; Shortis, 2015; Bryson et al., 2017; Raoult et al., 2017; Bayley et al., 2019; Marre et al., 2019). Ecological applications of photogrammetry, whilst rare, show that the accuracy and information-richness of resultant metrics affords more explanatory power of associated biotic communities than comparable manual methods such as chain-and-tape rugosity (Ferrari et al., 2017; González-Rivero et al., 2017; Urbina-barreto et al., 2020; Million et al., 2021). Therefore, it is an ideal time to establish practices of transparency of processing methods as well as standardization. Our routines are designed extract metrics simply and quickly minimizing manual input and decision-making on the part of the user.

Whilst we did not statistically analyze all the calculated metrics, the utility of each of these has been documented in the literature. Thus, researchers can select the most appropriate metrics for research questions from the suite provided by our code (see **Table 3**).

### Establishing the Ecological Utility of Structural Metrics

The metrics presented in this study can be used to compare various aspects of reef functionality by relating aspects of the shape of colonies to their size among different categorical growth forms simultaneously. Such approaches have been shown to be effective in estimating the functional capacity of reefs at the assemblage-scale (Urbina-barreto et al., 2020), predicting higher-order traits of corals using simple morphometrics (House et al., 2018), tracking reef responses to disturbance events (Zawada et al., 2019b), and measuring functional changes associated with colony growth (Million et al., 2021).

Comparison of two metrics of refuge provisioning among our sampled colonies revealed subtle differences in spatial refuge provisioning among a range of morphotaxa (**Figure 3**). We found that absolute spatial refuge could be predicted as a function of colony diameter and morphotaxa, despite a relatively small sample size for some coral groups. The power-law scaling relationships present among colonies are in agreement with other studies of 3D geometry at the colony



**FIGURE 3 | (A)** Plotted posteriors from linear model of shelter size factor from the interaction model containing colony diameter as a predictor for each of the seven morphotaxa. Shaded regions are 95% highest density probability intervals and solid lines are mean slopes of the mean from the posterior probability distribution. **(B)** Posterior predictions for intercept ( $\alpha$ ) and slope ( $\beta$ ) parameters in the same model. Circles indicate means, thick blue bars are 50% credible intervals, thin blue line are 95% credible intervals. All model coefficients including posterior uncertainty are available numerically in **Table S3**.

scale (Dornelas et al., 2017; Urbina-barreto et al., 2020). It is promising that historical data, collected when only 2D metrics were available, may be usefully compared with modern data to document changes overtime. It also suggests that where resource and time limitations prevent the gathering and processing of comprehensive suites of 3D data, for example in small-scale community reef management or citizen science scenarios, ecologically meaningful inferences could be drawn from the measurement of colony diameter and morphotaxa alone. However, whilst we found evidence here for strong scaling relationships between two and three-dimensional elements of colony geometry, our dataset was relatively small, and many

more colonies will be needed to solidify these relationships. Given enough data, a combination of the metrics presented here could be used as a platform to relate colony geometry not only to morphotaxa (as we did here) but also to environmental variables such as depth or exposure. This is arguably necessary as such variables have been shown to influence the phenotype of different coral taxa in the past (Todd, 2008; Ow and Todd, 2010; Doszpot et al., 2019).

Our results indicated that, contrary to Urbina-Barreto et al. (2020), tabular colonies did not provide greater volumes of spatial refuge among colonies of similar size from other morphotaxa. Further, the high surface area created by the

finely branching structure of the canopy itself depresses slightly the estimate of shelter size factor. Their generation of a single, large and continuous overhanging space below the ‘canopy’ has been shown to be a keystone reef structure, capable of supporting high biomass of a range of sizes of fish and other biota (Kerry and Bellwood, 2015). Whilst our generation of estimates for absolute spatial refuge and shelter size factor do capture in part the shaded overhang generated by tabular colonies (Figure S1), it is a conservative estimate of the space they generate. Depending on the growth orientation, vertical distance between the canopy and the benthos and canopy size, the refuge space generated by such morphotaxa can be considered highly variable, which should be a consideration when applying these metrics extraction routines in the future.

### Future Uses of Structural Complexity Metrics

Coral reefs are undergoing substantial change due to a combination of global (Hoegh-Guldberg et al., 2007; Hughes et al., 2017a; Hughes et al., 2017b; Williams and Graham, 2019), and local stressors (Suchley and Alvarez-Filip, 2018). Temperature-induced bleaching events cause differential mortality among coral taxa, with structurally complex taxa such as tabular and branching *Acropora* often being the most adversely affected (Wilson et al., 2006; Madin et al., 2014; Álvarez-Noriega et al., 2016; Hughes et al., 2019). It is expected that as shifts in community composition occur and the relative abundance of stress-tolerant, structurally simple species such as massive and submassive corals increases, reefs may have a reduced capacity to provide shelter spaces for fishes (Karkarey et al., 2017). Our hope is that others will generate data using the routines presented in this study to begin to build a repository of data containing information on many aspects of 3D colony geometry so that such contemporary questions as these can be answered effectively.

Some of the most practical future uses of the photogrammetry derived metrics presented here will be to measure colony growth and to relate aspects of their structure and size to the inhabitant fish species assemblages. Previous studies have found larger colonies support larger and more diverse fish assemblages even at these fine spatial scales, but these relationships are nuanced (Noonan et al., 2012; Agudo-Adriani et al., 2016). The use of photogrammetry scans to relate the full 3D structure of colonies to inhabitant fish is lacking (but see Agudo-Adriani et al., 2016) and establishing reliable relationships across the diverse suite of corals and fish will require large amounts of data from different study groups. Such information will be valuable to management and restoration efforts, where it is useful to know which specific combination of structural parameters leads to maximal biomass of the inhabitant fauna. Selection of coral species in restoration efforts should be tailored to include species that balance hardiness and survivorship with the ability to support fish through the provision of quality refugia (e.g. Shaish et al., 2010). There is a paucity of data across the literature on the 3D nature of growth among different colony morphotypes (but

see Million et al., 2021). Reimaging the same colonies at different time points and extracting a full suite of metrics such as those in this study could provide good insights into how various elements of coral structure changes over time when paired with suitable structural complexity metrics beyond simple linear extension.

### Considerations and Limitations of Photogrammetry-Based Metrics

Photogrammetry scans are, at present, the only way to obtain estimates of surface measurements of corals and the volume of generated habitat refuge at sub-centimetric resolution without disturbing/killing colonies. We were not able to compare underwater scans to control references due to the *in-situ* nature of this study, and thus could not empirically validate the accuracy of our surface measurements. However, studies validating the method using laser and/or computerized tomography (CT) scans of dead coral skeletons have found highly realistic representations (>90% similarity to laser scans) can be obtained even when scanning complex branching corals (McKinnon et al., 2011).

Most of the colonies in this study were <50cm maximum diameter, which does not capture the full range of sizes able to be obtained by all the included morphotaxa, so more data is needed these larger sized colonies. However, the larger reconstructed colonies (~1m diameter) that had associated photosets of >250 photographs were still well modelled in a few hours. The main constraint on the reliability of estimates of the generated in this study is the likely to be the complexity of the branching structures of complex colony shapes (Figueira et al., 2015). Photogrammetry scans are unable to model what is not seen by the camera lens, so occlusions caused by excessively complex/fine branching structures lead to incorrect representations of the 3D structure. The addition of more photographs overcomes this to an extent as excessive overlap between photographs leads to more detail in the surfaces of models, but as colonies become larger and more structurally complex, the model representations are susceptible to a reduction in accuracy (Bythell et al., 2001; Figueira et al., 2015; Zawada et al., 2019a).

### CONCLUSIONS

Photogrammetry is a suitable tool for assessing structural complexity at the colony scale. We show here the information richness and wide utility of photogrammetry by extracting 11 metrics of surface geometry and structural complexity using a single method. The semi-automated workflow presented in this study provides both new and experienced photogrammetry users with a tool to reconstruct corals at the colony scale, then extract an extensive suite of 3D structural complexity metrics. By automating processing at key steps, we aim to facilitate replicability and thus comparisons between studies, boosting the predictive power of statistical models over time

and building a repository of shareable 3D data. As more studies incorporate such routines into their 3D processing workflow, the potential to uncover the nature of how structure relates to function among coral morphotaxa to aid ecological interpretation is immense.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

EA designed the study under the supervision of SD and AH. Fieldwork was carried out by EA. EA performed statistical analyses, coded processing scripts and wrote the manuscript. All authors provided feedback and contributed to the editing of the manuscript, and approved the final submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.854395/full#supplementary-material>

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