



# Community composition predicts photogrammetry-based structural complexity on coral reefs

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**Abstract** The capacity of coral reefs to provide ecosystem services is directly related to their three-dimensional structural complexity. This parameter is also correlated with total fish biomass, reef resilience to external stresses and the dissipation of wave energy. However, information on structural complexity (i.e., reef rugosity) has not always been assessed in historical monitoring programs, and long-term trends are sometimes unavailable. In this study, we show that it is possible to predict and hindcast the three-dimensional complexity of coral reefs by combining photogrammetry, statistical modeling and historical benthic community data. We calibrated lasso generalized linear models and boosted regression trees to predict structural

complexity from photogrammetry transects around Moorea (French Polynesia). Our models were able to predict structural complexity with high accuracy (cross-validated  $R^2$  ranges between 0.81 and 0.9). We then used our models to hindcast historical trends in 3D structural complexity using community composition data collected in Moorea from 2004 to 2017. The temporal analysis highlighted the severe impact of a crown-of-thorns (COTS) outbreak from 2006 to 2009 and Cyclone Oli in 2010. In conjunction, these two events reduce coral cover from  $\sim 50\%$  to almost zero. While the collection of actual data is always to be preferred, our model captured these effects, confirming the capacity of this modeling technique to predict structural complexity on the basis of assemblage composition.

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## Introduction

The increasing frequency of coral mass mortality associated with bleaching events raises global concerns (Van Oppen and Lough 2009; Heron et al. 2016; Hughes et al. 2017). These disturbances are associated with severe habitat destruction, which reduces the structural complexity of coral reefs (Newman et al. 2015). Structural complexity is the three-dimensional spatial arrangement of an ecosystem (McCormick 1994; Chazdon 2014), and on coral reefs this is represented by the multitude of growth forms and distribution of hard corals. According to the habitat heterogeneity hypothesis, the more complex the structure of an ecosystem, the greater the diversity and abundance of associated organisms (MacArthur and Wilson 1967). On coral reefs, the 3D structural complexity of

the habitat is correlated with the biomass and diversity of fishes (Willis and Anderson 2003; Gratwicke and Speight 2005; Alvarez-Filip et al. 2009; Rogers et al. 2014), the reef's capacity to recover from disturbances (Graham et al. 2015) and the reef's ability to dissipate wave energy, thus protecting the shoreline from extreme inundations (Harris et al. 2018). Broad-scale declines in the complexity of coral reefs have been observed in the Caribbean and the Indo-Pacific as a result of both human impacts and climate changes (Hoegh-Guldberg 1999; Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Perry et al. 2018). While several monitoring programs (e.g., NOAA coral reef monitoring plan) regularly assess structural complexity, this is not the case in across all regions such as French Polynesia.

In the context of spatial analysis in geomorphology, Risk (1972) and Hobson (1972) highlighted the importance of selecting surface complexity metrics that are (1) readily understandable and interpreted, (2) capable of being measured in the field and (3) comparable among studies and locations. In early studies, it was proposed that rugosity could be recorded by draping a steel chain over the reef surface, then measuring the ratio between the total length of the chain and the planar distance between the ends of the chain. The higher the ratio, the more complex the substratum (Hill and Wilkinson 2004; Graham and Nash 2013). Despite the ease of use of such metric, laying a chain represents a bi-dimensional measure which does not capture three-dimensional (3D) habitats such as coral reefs. Although some time-consuming 3D metrics have been proposed (e.g., Parravicini et al. 2006), recent progress in underwater photogrammetry only recently provided the opportunity to capture the three-dimensionality of coral reefs. Examples of studies that employ photogrammetry include the use of a remote-operated vehicle (ROV) equipped with a downward-looking camera (Friedman et al. 2012), extracting the species-level complexity index for six species along a transect (Burns et al. 2015), defining new metrics to estimate complexity such as tortuosity and fractal dimension (Leon et al. 2015; Naughton et al. 2015) and measuring the small-scale three-dimensional features of a shallow-water corals with drones (Casella et al. 2017). The growing prevalence of photogrammetry in studies on structural complexity has led some researchers to question the chain-tape method (Storlazzi et al. 2016).

Whatever the metric employed (chain-tape or photogrammetry), ample data demonstrate that corals contribute to the overall complexity of a reef, but the mechanism by which corals contribute to this complexity is still a matter of debate. Some authors claim that it is driven by the presence of branching species such as *Acropora* spp., and overall coral cover is not as important (Aronson and Precht 2006; Alvarez-Filip et al. 2009, 2011). Others

claim that coral cover is significantly and highly correlated to rugosity (Halford et al. 2004; Graham and Nash 2013) and/or species composition (Richardson et al. 2017). In both cases, there is a consensus that structural complexity is related to coral community structure.

In this study, we combined statistical modeling with the reconstruction of 3D reef transects via photogrammetry in order to test our capacity to predict coral reef structural complexity on the basis of benthic community composition. Using benthic time-series data, we back-calculated reef structural complexity since 2004. We were able to retrace two relevant episodes of habitat destruction: the COTS outbreak from 2006 to 2009 and Cyclone Oli in 2010.

## Materials and methods

### Study area

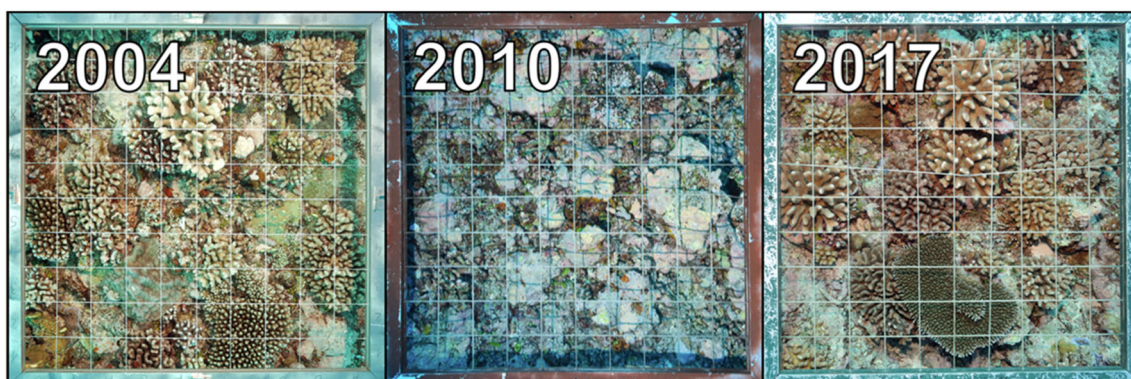
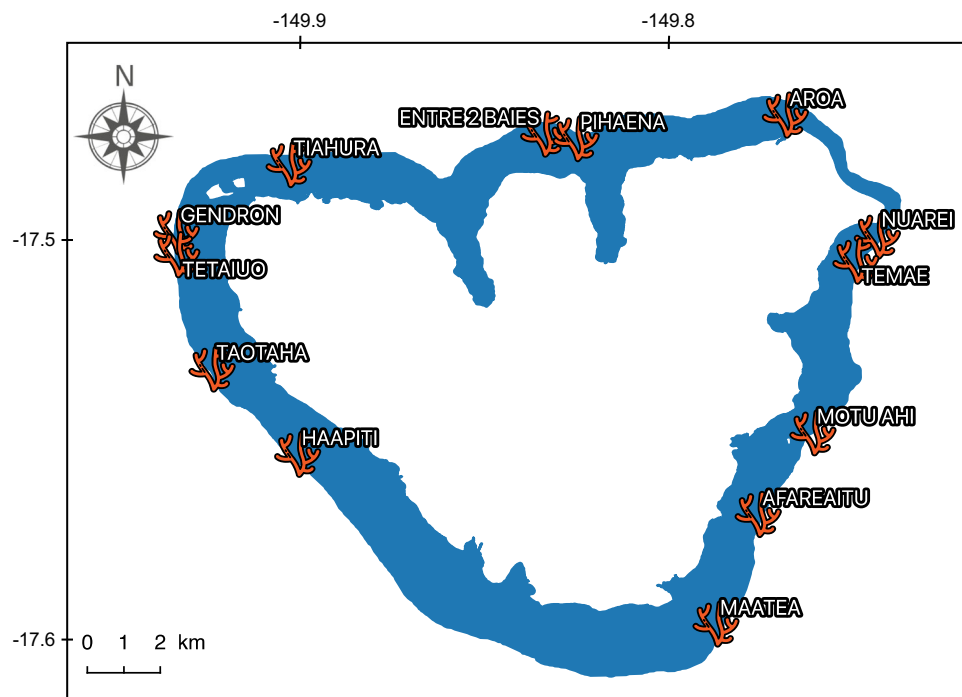
Moorea (French Polynesia) is located in the Pacific Ocean between 17.4714° and 17.6058° south and 149.7522° and 149.9269° west. The island has three coastlines which face to the north, southwest and southeast (Fig. 1). The island is encircled by a coral reef, which is 500–700 m wide. The only exception is the northeast extremity where the lagoon width is limited to a few tens of meters. Tides are semidiurnal with an amplitude of less than 0.3 m (Chazottes et al. 1995; Leichter et al. 2013). The swell direction is from the southwest to northeast during the entire year. The three sides of the islands can thus be used as a proxy of wave exposure (Carroll et al. 2006).

The reefs in Moorea are threatened by several biotic and abiotic disturbances (Adjeroud et al. 2018). The most devastating biotic disturbances were the 1979 and 2006 COTS outbreaks, each of which reduced average coral cover from 50 to 10% or less (Berumen and Pratchett 2006; Lamy et al. 2016). Cyclones are the primary abiotic disturbances that affect reefs around Moorea. In 1991, Cyclone Wasa reduced coral cover around Moorea from 20 to 5%, while Cyclone Oli reduced coral cover, which was still recovering from the COTS outbreak, from 7 to 3% in 2010 (Lamy et al. 2016; Adjeroud et al. 2018) (Fig. 2).

### Structural complexity measurements

In Moorea, 57 photogrammetric transects were surveyed from the end of 2015 through the beginning of 2016 at three different sites that correspond to three wave exposures: Tiahura (North coast, 21 transects), Haapiti (Southwest coast, 20 transects) and Temae (Southeast coast, 16 transects) (Fig. 1). Surveys were run as 20 m × 2 m belt transects, and all transects were conducted on the outer reef

**Fig. 1** Location of the thirteen long-term monitoring sites surveyed each year from 2004 until 2017 around Moorea in the Society archipelago, French Polynesia



**Fig. 2** Evolution of one of the twenty quadrats used to define coral cover in Haapiti (on the southwestern side of the island) before (2004), immediately after (2010) and several years after (2017) Cyclone Oli

between 5 and 8 m depth. For each transect, a 2-m-long chain was placed perpendicularly to a 20 m transect, then a diver swam  $\sim 2$  m above the benthos along the transect at a constant speed as constant while collecting images with a GoPro Hero4 camera pointed toward the benthos. The camera was set to collect photographs (12 megapixels) in time-lapse mode (2 pictures per second). For each transect, we collected approximately 300 photographs with a forward overlap of  $\sim 90\%$ , with the diver swimming over the length of the entire transect four times to allow optimal side overlap. After the photograph collection, the diver noted the depth of each extremity of the chain and transect tape so that they may be used as ground control points (GCPs). In the case of an in situ self-calibration, the camera calibration is derived from image coordinates measured in

the mapping photography and including the camera calibration parameters as unknown in a self-calibrating bundle adjustment (Harwin et al. 2015).

The photographs and the GCPs were input into Agisoft Photoscan ([www.agisoft.com](http://www.agisoft.com)), a photogrammetry software based on the structure from motion (SfM) method (Ullman 1979; Westoby et al. 2012). We used Agisoft to build the orthophotomosaic and the digital elevation model (DEM) of each transect, as explained by Storlazzi et al. (2016). For the 57 transects, we estimated an average horizontal error of  $0.1 \pm 0.06$  m and an average vertical error of  $0.04 \pm 0.04$  m. Only the vertical error influenced the estimation of rugosity, but given the range of the error, it was considered negligible. Details of the photogrammetric process are detailed in Annex S1. Subsequently, we

imported the DEM in ArcGIS v10.2 and calculated reef rugosity by dividing the surface of the DEM area by the area of its planar projection (approximately 40 m<sup>2</sup>) (Fig. 3).

### Benthic community description and assessment

In order to predict structural complexity as a function of benthic community structure, the orthophotomosaics produced by Agisoft Photoscan were imported into the software Coral Point Count v4.1 (Kohler and Gill 2006). We assessed benthic cover by placing 100 random points on the photomosaic and described 8 distinct benthic cover categories (Table 1).

In order to hindcast structural complexity for the three sites surveyed around Moorea, data from the MPA network long-term monitoring program were used. This dataset consists of benthic surveys from 2004 to 2017 using 25 m line-point intercept transects collected around the island across three habitats (fringing reef, back reef and outer reef) (Fig. 1). For comparability among datasets, we used only the long-term monitoring data collected on the outer reef.

### Statistical analysis

All the statistical analyses were run on R version 3.5.3 (R Core Team 2019). Our main goal was to calibrate a model that predicts structural complexity according to benthic community composition. In order to achieve this, we built a database that includes the time series data and data from our photogrammetry transects without transforming the data to perform multivariate analysis. Thus, the Euclidean distance on untransformed data was used to generate a principal component analysis (PCA) using the *vegan* package in R. The first five orthogonal axes, which accounted for more than 75% of the variance, were then extracted as predictor variables. To account for spatial variability in exposure, we included island side (north, southwest, southeast) as a parameter in our model.

**Table 1** Shape classification categories defined to estimate rugosity

ACR	<i>Acropora</i> spp.
CCA	Crustose coralline algae
DEA	Dead corals
ENC	Encrusting corals
SMU	Sand and mud
RUB	Rubble
MAC	Macroalgae
MAS	Massive corals
OER	Corals with other erects forms
OTH	Other (like echinoid)
PAV	Pavement, bare rock and turf covering rock
POC	<i>Pocillopora</i> spp.

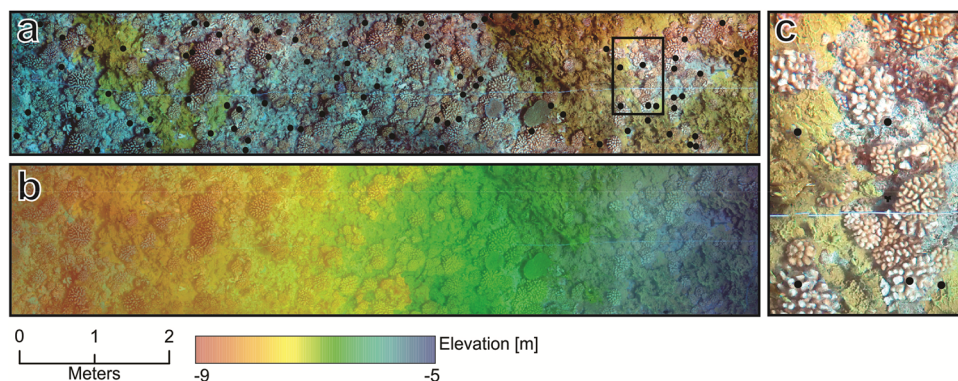
Ten variables are morphological, but the genus level is given for *Acropora* spp. and *Pocillopora* spp

In our models, we used lasso generalized linear models (using the *caret* package in R) and boosted regression trees (BRT; Elith et al. 2008). With both methods, model selection was done to maximize the deviance explained with a tenfold cross-validation procedure ( $CV-R^2$ ). More precisely, the dataset is split into ten sections, nine of which are used for the calibration, and the last one is used for the evaluation of model performance.  $CV-R^2$  represents the expected performance of the model when fitted to new data (Elith et al. 2008).

In the model, coral reef structural complexity was predicted by the five PCA axes and island side as a proxy of wave exposure. In addition, BRT were fitted using the R functions provided by Elith et al. (2008). This technique requires the specification of four main parameters: bag fraction (bf), learning rate (lr), tree complexity (tc) and the number of trees (nt), where bf is the proportion of samples used at each step, lr is the contribution of each fitted tree to the final model, tc is the number of nodes of each fitted tree and nt represents the number of trees corresponding to the number of boosting iterations. Optimal parameters were selected by  $CV-R^2$  maximization (Parravicini et al. 2013).

**Fig. 3** Example of underwater photogrammetry.

**a** Orthorectified photomosaic. The black dots indicate the random points with shape classification. **b** Digital elevation model representing depth values (the photomosaic is kept transparent in the background). **c** Detail of the photomosaic



The models were calibrated using 1000 bootstrap replicates of the original dataset to estimate uncertainty and provide 95% confidence interval around predicted values.

Both models were then used to hindcast structural complexity since 2004 using time series data. In order to estimate whether predicted structural complexity was able to identify the effect of major past perturbations (i.e., COTS and Cyclone Oli), we generated PCAs for each year using the Euclidean distance on untransformed data. We chose running PCAs to emphasize the patterns driven by the most abundant species/taxa (i.e., the ones with the highest percent cover) since PCAs are more sensitive to variations in abundance than other ordination analyses (Van den Boogaart and Tolosana-Delgado 2013). For the purpose of this study, we conducted a CA to verify that results are consistent. We ran an analysis of variance with year and island side as fixed factors to test for differences in structural complexity. A Tukey post hoc analysis was then used to compare structural complexity across individual years.

## Results

The time series data revealed that coral diversity was higher in 2004, with an average percent coral cover (CC) of 44.08% (Fig. 4). The CC decreased from 2004 to 2010, reaching a minimum of 3.62% CC, which corresponds to Cyclone Oli. After that, the CC increased through 2017, with a final value of 42.77%. In 2004, the coral reefs around Moorea also showed a higher diversity of coral morphologies (massive, branching, columns and encrusting). The assemblages remained fairly stable despite a slow decline of CC from 2004 to 2006 (44.08–40.62%). Then, a first COTS outbreak occurred in early 2006 and continued until 2009 (Kayal et al. 2012). The following year, Cyclone Oli, hit the island, further decreasing CC. After these events and until 2014, the substrate predominantly consisted of rubble. From 2015, the CC recovered to a state similar to that of 2004. However, compared to 2004, the coral cover in 2017 had a lower percent cover of *Acropora* spp. ( $9.76 \pm 5.61\%$  in 2004 vs  $2.53 \pm 1.90\%$  in 2017). In contrast, the percent cover of *Pocillopora* spp. remained fairly stable ( $20.10 \pm 6.78\%$  in 2004 vs  $26.61 \pm 14.52\%$  in 2017).

The cross-validated  $R^2$  (CV- $R^2$ ) from our models reached 0.81 for the lasso GLM and 0.9 for the BRT. After model selection, the first three PCA axes and island side were retained by the lasso GLM, and all variables were kept by the BRT (Table S2, Fig S1). The back calculation of structural complexity captured all major shifts in community structure described above. All sites were predicted to lose complexity in synchrony with COTS outbreaks and

Cyclone Oli (Fig. 5). Further, structural complexity also differs according to wave exposure.

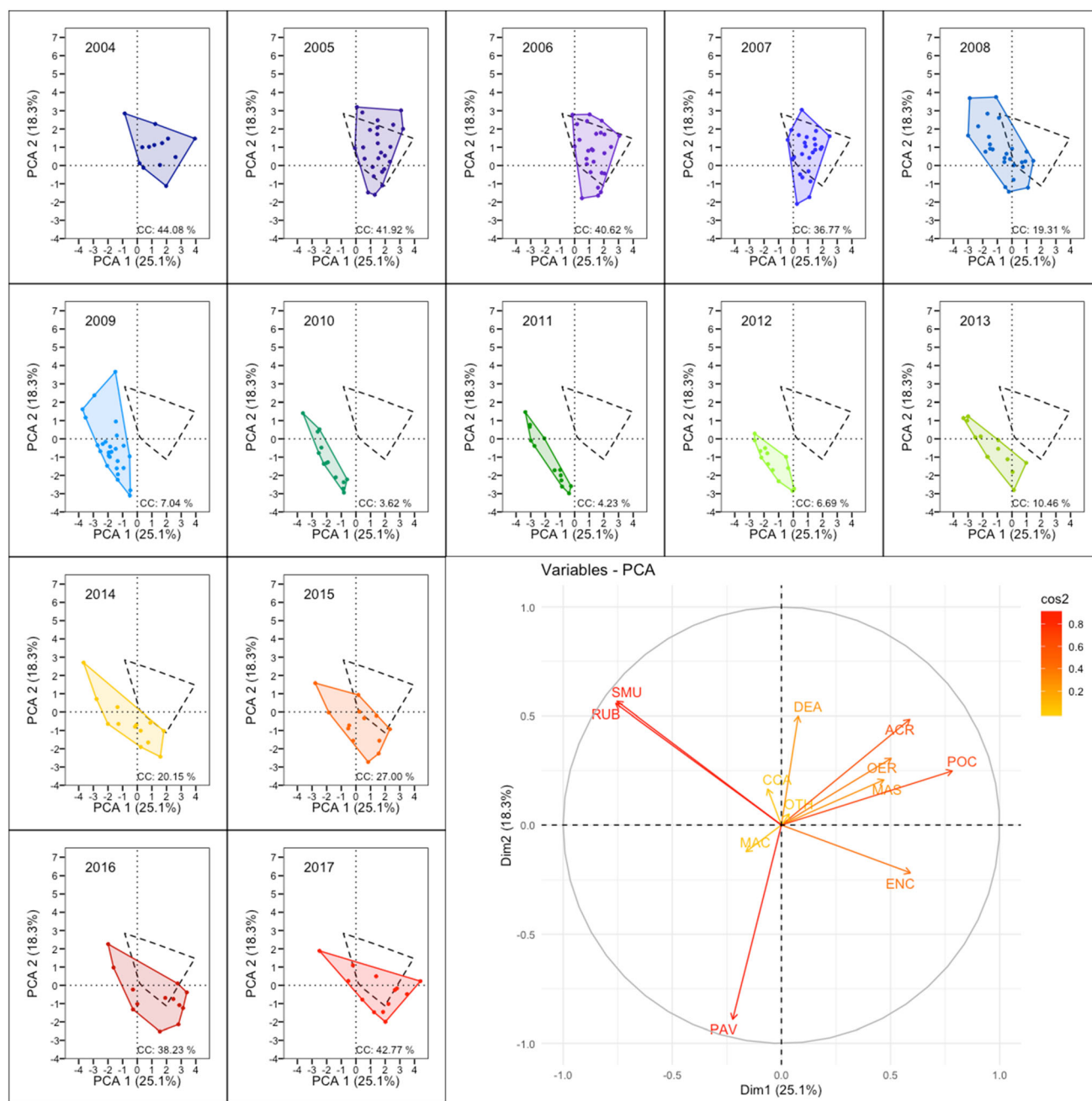
Finally, rugosity reached pre-disturbance levels in 2015. Then, at the scale of Moorea, structural complexity remained fairly stable. Indeed, despite local differences, when we compare the first year of monitoring (2004) with the last year of monitoring (2017), no significant differences were detected (Fig. 6, Table S1).

## Discussion

Utilizing a combination of photogrammetry and statistical modeling, we were able to use long-term species composition data to predict the structural complexity of coral reef assemblages around Moorea over the course of 14 years. Our hindcasted metric of structural complexity captured the significant changes in coral cover observed on Moorea's coral reefs (Berumen and Pratchett 2006; Adjeroud et al. 2018). *Acropora* spp. and *Pocillopora* spp. were dominant in 2003 and 2004 (Berumen and Pratchett 2006). Subsequently, the populations of these genera were affected by both COTS outbreaks (2006–2010) and Cyclone Oli (2010) (Kayal et al. 2012). *Acropora* was primarily susceptible to these disturbance events, but *Pocillopora* also eventually collapsed, followed by *Montipora* and *Porites*. During these events, predicted structural complexity dropped across all sites, demonstrating that statistical models can produce reasonable predicted values when accrual data are not available.

The use of photogrammetry allowed us to obtain a three-dimensional metric of structural complexity, which contrasts to the traditional chain transect method (Burns et al. 2015). Alvarez-Filip et al. (2009) reviewed 464 records of rugosity among 200 reefs, which were predominantly performed with the chain method. None of the reported measures exceeded a rugosity of 4; however, 7% of our measurements exceeded this value. This may simply be attributed to the specific characteristics of our study, or, more likely, it may result from the higher resolution of photogrammetry compared to the chain method. Although a higher resolution (pixel size of  $1.73 \mu\text{m} \times 1.73 \mu\text{m}$ ) does not translate to higher accuracy, it is important to also be aware of the limitations of photogrammetry (Figueira et al. 2015; Lavy et al. 2015; Bryson et al. 2017). For example, the use of photogrammetry performs better on planar segments of the reef where the diver can easily maintain a fixed distance from the benthos.

Our approach assumes that the confidence with which a model predicts structural complexity depends on several factors: (1) The calibrating dataset covers all the potential combinations of benthic community structure, (2) the predicted values are insensitive to the employed modeling



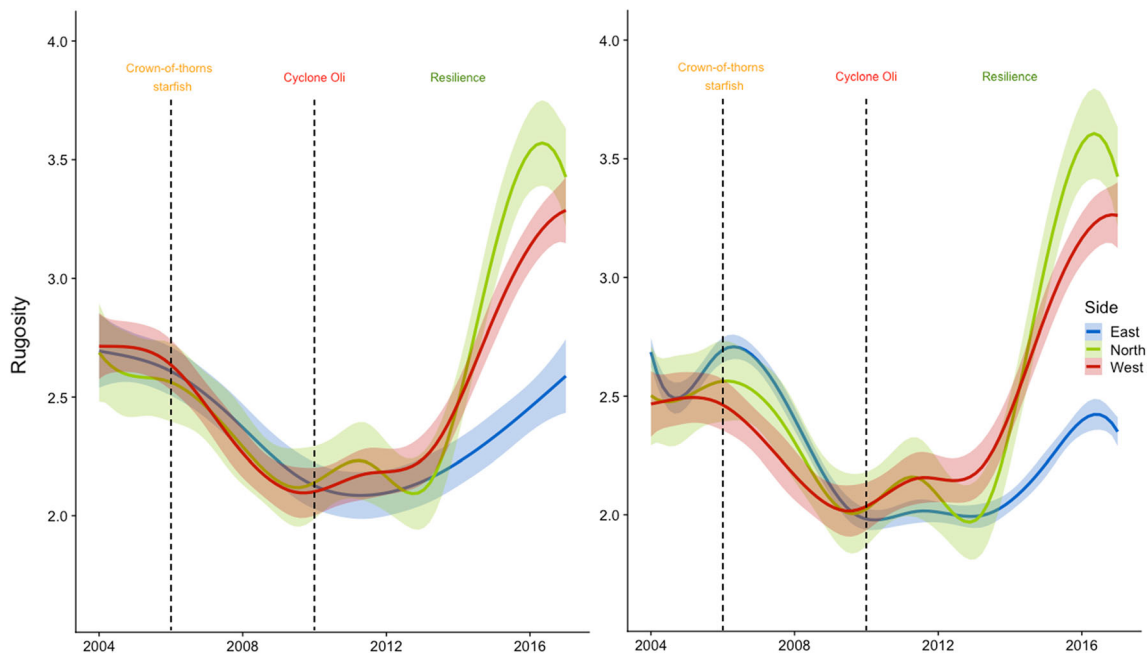
**Fig. 4** Principal components analysis (PCA) of the 11 morpho-species from 2004 to 2017. Coral cover (CC) is written at the bottom right of each box. On each plot, the coral community in 2004 is included as a baseline in black dashed lines. Abbreviations are as follows: ACR—*Acropora* spp; CCA—crustose coralline algae;

DEA—dead coral; ENC—encrusting corals; MAC—macroalgae; MAS—massive corals; OER—other erects forms; OTH—others (Sponges or benthic species); PAV—pavement; and POC—*Pocillopora* spp; RUB—rubbles; SMU—sand or mud

technique, (3) the model performs well on new data not included in the calibration, and (4) the model performance is insensitive to small variations in the input dataset. Statistical techniques allow us to address the last three points. Here we accounted for the uncertainty related to the statistical technique (i.e., comparing BRT vs. GLM) and the effects of small variations in the input dataset using

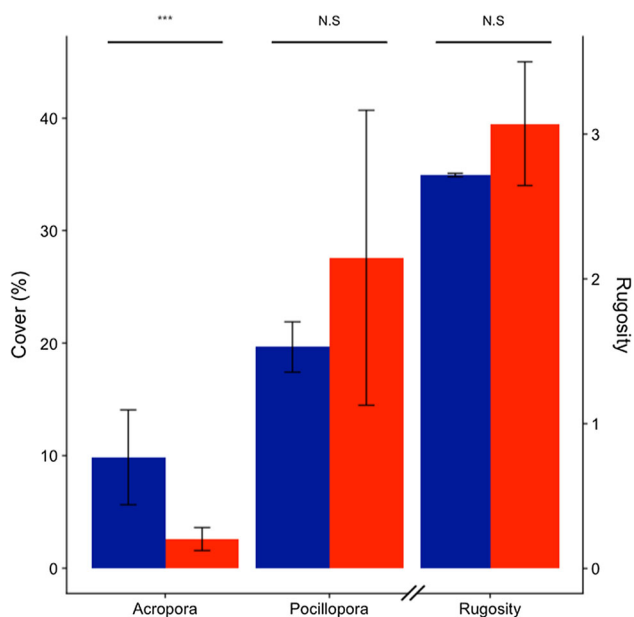
bootstrapping, and we evaluated the performance of our model on new data with cross-validation. Upon doing this, uncertainty can be estimated and propagated into further analyses if structural complexity is used as a covariate in subsequent models.

Although the collection of actual data is preferred to hindcasting, when structural complexity information is not



**Fig. 5** Rugosity reconstructions from 2004 to 2017 according to the average of the models (cross-validated generated trees boosted model on the left and cross-validated lasso generalized linear model on the

right) on each of the three sides of Moorea. The COTS outbreak and Cyclone Oli are shown in 2006 and 2010, respectively



**Fig. 6** Difference between *Acropora* and *Pocillopora* cover (%), as well as the difference in rugosity index. Dark blue bars represent 2004, and red bars represent 2017. Asterisk indicates significant differences ( $p < 0.05$ ) while N.S indicate non-significant differences ( $p > 0.05$ )

available and ‘reference’ or historical conditions need to be determined, statistical modeling can be used with caution to complement to existing data. However, predicted values from models cannot be blindly accepted. First, while the space-for-time approach is frequently used in ecological

research (Pickett 1989; Mcclanahan and Graham 2005; Done et al. 2010; Van Woesik et al. 2011), it is prone to potential biases (Kappes et al. 2010). For example, dead coral can dominate benthic communities after a COTS outbreak as well as after a cyclone, but the 3D structure of the assemblage will be different in these two cases. Indeed, in both cases, live coral cover will be low, but after a COTS outbreak, the 3D structure of corals will be maintained; on the contrary, after a cyclone, the community will be flattened. Unfortunately, our calibrating dataset did not include data collected during perturbed conditions, such as after Cyclone Oli. Second, our calibrating dataset only included 5% acroporid cover, while in 2004, *Acropora* cover was, on average, 10%. Therefore, while we are able to delineate the general temporal trend, our capacity to accurately predict rugosity during these conditions is limited. Finally, topography may vary across time as a result of the balance between accretion and erosion, and topographic change may influence structural complexity in a way that cannot be accounted for in statistical models.

Structural complexity is negatively correlated with algal cover and strongly related to fish biomass, and it is also the main predictor of coral reef recovery after an acute disturbance (Graham and Nash 2013; Graham et al. 2015). Given the importance of structural complexity for the ecological functioning of coral reefs, the reconstruction of this variable from long-term benthic monitoring data may help us to better understand and predict changes in coral reefs. Today more than ever, global coral reefs are

witnessing the effects of climate change and other human impacts (Hughes et al. 2018). Coral bleaching is occurring on coral reefs with an unprecedented frequency, and future coral reefs are expected to lose diversity and productivity by these perturbations and effectively become flattened (Alvarez-Filip et al. 2009). Long and reliable time series are one of the best ways to obtain reference conditions for ecological indicators. When this information is not available, modeling represents a valuable alternative to track and anticipate the long-term loss of structural complexity.

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#### Compliance with ethical standards

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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