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Underwater photogrammetry reveals new links between coral reefscape traits and fishes that ensure key functions

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Abstract

Maintaining key functions of coral reefs is vital for the persistence of these ecosystems as well as for securing the goods and services that they provide in the Anthropocene. Underwater photogrammetry by Structure from Motion (SfM) allows the quantification of novel habitat descriptors that may be particularly relevant in assessing key reefscape traits, that is, physical and ecological characteristics of coral reef habitats. Here, we combined this new technology with fish surveys to explore how reefscape traits shape the functional structure of reef fish assemblages around three environmentally contrasted islands of the Indo-Pacific (Europa Island, Reunion Island, and New Caledonia). At 24 sites, habitat descriptors were computed from digital elevation models (DEM) and orthomosaics, while reef fish assemblages were assessed by visual census and video footage. Four habitat descriptors were marginally correlated and presented low variance inflation factor (VIF) values, thus being the most complementary descriptors: surface complexity, total shelter capacity, Shannon Shelter Index, and total coral cover. Linear mixed models (LMM) were used to explore the relationships between these habitat descriptors and four key fish functional entities: prey, planktivores, grazers, and predators. For each model, the variance explained (i.e., marginal R^2) was significantly higher when considering multiple predictors, including the novel three-dimensional descriptors (i.e., total shelter capacity and Shannon Shelter Index). The habitat descriptors quantified from underwater photogrammetry outputs (i.e., DEM and orthomosaics) provide easily available data to assess key reefscape traits and predict fish assemblage structure in coral reef ecosystems. This trait-based functional approach allows consistent assessment of the links between these descriptors from local to regional scales. Considering the global coral reef crisis

Isabel Urbina-Barreto and Simon Elise contributed equally to this study.

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and the increasing availability of world-reef photogrammetric surveys, this new technology should be key to bringing solutions to 21st-century conservation issues.

KEYWORDS
Anthropocene, coral reefs, digital elevation model, fish assemblages, habitat descriptors, key ecosystem functions, orthomosaic, photogrammetry, shelter capacity, structural complexity

INTRODUCTION

Identifying the key ecosystem functions that maintain coral reefs is a prerequisite to promote their future persistence and the sustainability of the goods and services they provide (Bellwood et al., 2019; Hughes et al., 2017). Over the last two decades, the understanding of coral reef functioning has been improved by considering the diversity and distribution of key eco-morphological traits of corals and reef fishes (Bellwood et al., 2004; Darling et al., 2012; Madin et al., 2016; McLean et al., 2021). For example, trait-based approaches for corals have improved proxies for key biological and ecological processes and already help fill data gaps by prioritizing easily measurable traits (Madin et al., 2016; McWilliam et al., 2018; Zawada, Dornelas, et al., 2019). Yet, the most widespread survey methods still focus on measuring overall coral cover to monitor the ecological status of coral reefs and inform conservation strategies (Hill & Wilkinson, 2004; Loya, 1972; Obura et al., 2019).

Introduced in the second half of the twentieth century, these methods rely on visual quantitative (e.g., line intercept transect method [LIT], point intercept transect method [PIT]) and semi-quantitative assessments (e.g., Dahl quotation, medium-scale approach [MSA]) of benthic characteristics along transects or within quadrats (Dahl, 1981; English et al., 1997; Goreau, 1959; Loya, 1972; Riedl, 1980). The main limitations of these methods are the need for biological expertise on the field, the lack of standardization due to variable expert competences, their limited representativeness of meso-scale distribution patterns, and the scarcity of the descriptors produced (Lam et al., 2006; Leujak & Ormond, 2007). Nonetheless, the use of photoquadrats and video transects has partially addressed these limits (e.g., Lam et al., 2006; Leujak & Ormond, 2007; Molloy et al., 2013). In parallel, the importance of measuring physical features to describe the structural complexity of coral reefs has been identified early and a wide range of methods have emerged toward this end (Graham & Nash, 2013; Wilson et al., 2007). Among them, the "chain and tape method" to measure reef rugosity (e.g., Risk, 1972; Friedlander & Parrish, 1998), the count and measurement of holes (e.g., Friedlander & Parrish, 1998; Gratwicke & Speight, 2005; Johansen et al., 2008), or the visual estimation of complexity on semi-quantitative scales (e.g., Darling et al., 2017; Gratwicke & Speight, 2005) has been variably used. Given the diversity of protocols, their strong dependence on observer capacity, and the lack of standardization, the monitoring of reef structural complexity is still not a standard component of conservation programs (Graham & Nash, 2013; Hill & Wilkinson, 2004; Obura et al., 2019).

Emerging technologies such as LIDAR and airborne imagery (Asner et al., 2020; Collin et al., 2018; Wedding et al., 2019), three-dimensional (3D) scanning (Reichert et al., 2016), or photogrammetry (Burns et al., 2015; Lange & Perry, 2020) can help fill these gaps. For example, they allow the computation of ecological and physical descriptors of benthic assemblages at multiple spatial scales, including descriptors not easily assessed through visual surveys. In particular, photogrammetry by Structure from Motion (SfM) technique, that is, the reconstruction of three-dimensional objects from a series of overlapping 2D images (e.g., photographs), has become a powerful and affordable tool for 3D topographic modeling and its geoscience applications (Westoby et al., 2012). Beyond 3D models, photogrammetry by SfM can provide digital elevation models (DEM; i.e., digital representation of a continuous surface with terrain elevation data) and orthomosaics (i.e., mosaicked image geometrically corrected such that the scale is uniform). Photogrammetric outputs have been analyzed to quantify a large range of reefscape traits, by considering both ecological (e.g., coral cover, shelter volume, colony size, and abundance) and physical descriptors (e.g., slope, surface complexity, fractal dimension) (e.g., Burns et al., 2015; Casella et al., 2016; Figueira et al., 2015; Fukunaga, Burns, et al., 2020; Torres-Pulliza et al., 2020; Urbina-Barreto, Chiroleu, et al., 2021a; Zawada, Dornelas, et al., 2019; Zawada, Madin, et al., 2019). With the multiplication of available descriptors, their relationships are increasingly explored to identify those most suited to capture the essential reefscape traits (e.g., Fukunaga et al., 2019; Fukunaga, Burns, et al., 2020).

As for corals, some of the functions ensured by fishes are crucial for coral reef stability and resilience (Bellwood et al., 2003; Green & Bellwood, 2009), and fish assemblages are increasingly studied from a functional

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point of view. Particularly, functional entities (FEs), which are defined on the basis of shared traits among species (e.g., diet, size, mobility, or schooling behavior; Guillemot et al., 2011), are considered to represent proxies for the functions ensured by groups of species. Functional entities have proven relevant for the assessment of fish vulnerabilities in the face of global threats (e.g., Graham, Chabanet, et al., 2011), in the identification of management targets (e.g., McClanahan, 2014), and in the description of worldwide biogeographic patterns (e.g., McLean et al., 2021). Others have investigated the links between fish FEs and habitat features, including visually assessed physical and ecological descriptors (e.g., Alvarez-Filip et al., 2011; Darling et al., 2017; Floeter et al., 2007; Friedlander & Parrish, 1998; Pinca et al., 2012). By combining accuracy and standardization of habitat assessment, emerging technologies offer great opportunities to re-examine these relationships and advance the understanding of fish–habitat functional relationships.

The taxonomic composition of coral reef fish assemblages is geographically variable and especially within large regions such as the Pacific Ocean. For example, Pinca et al. (2012) found only 1% of the species common to all the assemblages across 18 archipelagoes in the south and central Pacific. Such differences hamper comparisons of fish assemblage structure and fish–habitat relationships between distant locations. In contrast, the functions ensured by corals and fishes are relatively similar worldwide (McLean et al., 2021; McWilliam et al., 2018). Hence, surveys considering coral growth forms and fish FEs can be compared within and between regions, and the relationships between fishes and their habitat analyzed across wide geographical gradients. As such, trait-based approaches can strongly enhance global coral reef conservation strategies (Bellwood et al., 2019; Hoegh-Guldberg et al., 2018; McLean et al., 2021).

However, understanding the links between new quantitative habitat descriptors and the structure of fish assemblages was limited until now to a few species or coarse taxonomic descriptors, such as overall diversity or biomass (González-Rivero et al., 2017; Wedding et al., 2019). Only the studies of Agudo-Adriani et al. (2019), Fukunaga, Kosaki, et al. (2020), and Fontoura et al. (2020) focused on such relationships by combining taxonomic and functional descriptors of fishes (i.e., trophic or size structure of fish assemblages), highlighting the importance of multiple habitat descriptors, but also the need for further investigations. In particular, identifying habitat descriptors (beyond coral cover) that promote biodiversity and ensure functional fish assemblages could dramatically help the detection and conservation of favorable reef areas, and provide guidelines to selecting sites for resource conservation and restoration efforts. In the context of accelerating worldwide ecological disruption of coral reef ecosystems, conservation and management programs urgently need accurate holistic information to enhance actions that promote ecosystem regeneration (Duarte et al., 2020). As such, new descriptors could complement current programs that use physical and ecological aspects to estimate the resilience or vulnerability of coral reef ecosystems (e.g., Reef Resilience Network—www.reefresilience.org).

Here, we explored (1) the complementarity and redundancy among new quantitative habitat descriptors obtained by photogrammetry to select the most informative descriptors; (2) the relationships between these descriptors and the diversity, abundance, and biomass of key fish functional entities. Our main goal was to enhance our understanding of reef ecosystem functioning in support of improving coral reef stewardship.

MATERIALS AND METHODS

Study sites

Our study was conducted from July 2017 to April 2019 at 24 outer reef slopes sites around three islands: Europa and Reunion in the South-West Indian Ocean, and New Caledonia in the South-West Pacific Ocean (Figure 1). The sites encompassed coral reefs with strong environmental contrasts and a range of anthropogenic pressures. By example, there are about 350 inhabitants/km^2 of reef in Reunion Island, about 15 in New Caledonia, and <1 in Europa Island. The latter benefits from decades of strong protection and can be considered as a "nearly pristine" site. Fishing pressure is very high in Reunion, low to moderate in New Caledonia, and absent in Europa. Moreover, coral reefs are much younger at Reunion and Europa islands than at New Caledonia, which explains that outer slopes are located at a few hundred meters from the shore at Reunion and Europa, and at about 20 km at New Caledonia. This proximity, in turn, determines variable terrestrial influences at these three localities. Finally, most of the sites sampled at Europa Island were less exposed to wind and waves than those sampled at the other two islands.

Three-dimensional reconstructions and assessment of reefscape traits

Reefscapes were 3D modeled by photogrammetry using a consistent protocol across the 24 sites, following the workflow proposed by Urbina-Barreto, Chiroleu, et al. (2021a). Images were collected on SCUBA to

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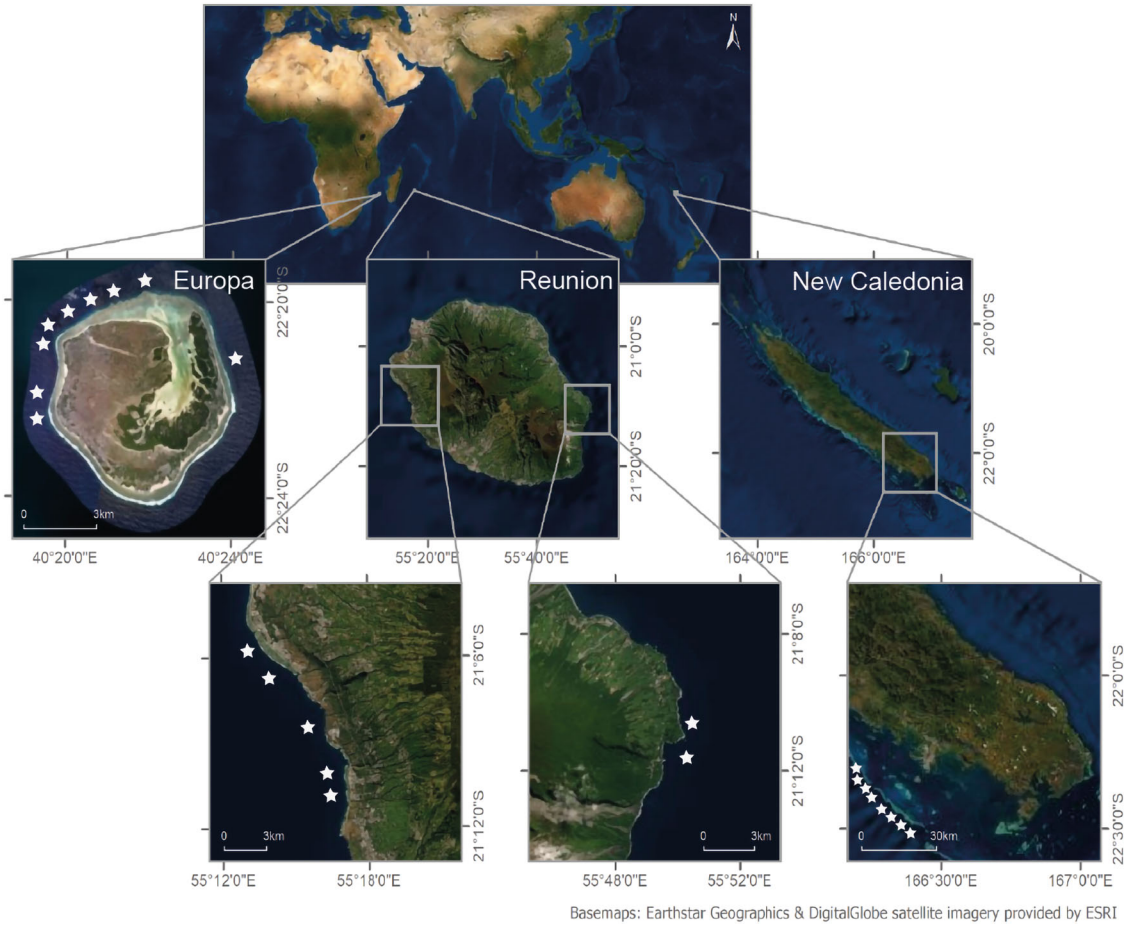

FIGURE 1 Location of the 24 study sites (white stars) on the outer reef slopes of Europa, Reunion, and New Caledonia. At Reunion, sites on the east coast were located on lava flows

cover an area of 150 m^2 (15 × 10 m patch) at ~14 m depth. Images were taken in a boustrophedonic pattern along several parallel lines 3 m above, and oriented perpendicular to, the seafloor. Additional oblique images were taken for high-complexity reef components. Mean overlap among images was ~70%. Depending on topography and structural complexity, between 500 and 1300 images were taken at each site.

Three-dimensional models were constructed using Pix4Dmapper Pro software (v4.2.26). The mean resolution of the models (i.e., ground sampling distance) was 0.13 cm/pixel, and the mean reprojection error was 0.25 pixel (i.e., the distance between the marked and the reprojected point on one image for each computed 3D point—https://support.pix4d.com). Digital elevation models (DEMs; i.e., digital representation of a continuous surface with terrain elevation data) and orthomosaics (i.e., geometrically corrected mosaicked images with a uniform scale) were generated and clipped to a plane area of 150 m^2 in Global Mapper v19.0 software (Blue Marble Geographics, 2019) to perform physical and ecological analyses.

Scleractinian coral colonies were manually delineated as polygons (by drawing edges of colonies) on the orthomosaics using the open source GIS software QGIS (version 3.4.6 Madeira, QGIS Development Team, 2019), considering an individual as a colony growing independently from its neighbor (Loya, 1972). Each colony was classified by growth form following Veron (2000): branching, columnar, encrusting, foliaceous, helmet-shaped, tabular, massive, and free-living. Other benthic organisms (i.e., soft corals, Milleporidae, crustose coralline algae) and abiotic components (i.e., sand and rubble) were delineated but not analyzed here (Appendix S1: Figure S1). To measure the main reefscape traits at each study site (Table 1, Figure 2), 22 habitat descriptors were computed as follows:

DEM descriptors

Surface complexity (i.e., the ratio of 3D surface/2D surface), fractal dimension, and mean slope were computed in R (R Core Team, 2021) using functions in Fukunaga et al. (2019).

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TABLE 1 Main reefscape traits and corresponding units by groups of habitat descriptors: Digital elevation model (DEM) descriptors (from DEM analyses), surface descriptors (from orthomosaics analyses), mapping descriptors (from orthomosaics analyses), and three-dimensional (3D) descriptors (from shelter predictive models)

Groups of descriptors	Reefscape traits	Units	Justification
DEM descriptors	Surface complexity (3D/2D surface)	Ratio (unitless)	Surface complexity is the 3D transposition of "traditional" rugosity measurement (Risk, 1972), which has been shown to positively influence the diversity, abundance, and biomass of fish assemblages and enhance the resilience of reef ecosystems. (Darling et al., 2017; Friedlander et al., 2003; Graham & Nash, 2013). R code is available for its standardized and easy calculation (Fukunaga et al., 2019)
	Fractal dimension (FD64 from Fukunaga et al., 2019)	Index (unitless)	Fractal dimension is the second historical descriptor (after rugosity) mostly used to describe habitat complexity (Bradbury & Reichelt, 1983; Burns et al., 2019; Mark, 1984; Young et al., 2017). R code is available for its standardized and easy calculation (Fukunaga et al., 2019)
	Mean slope	Degrees (°)	Slope angle enhances both coral and fish diversity (Newman et al., 2015). R code is available for its standardized and easy calculation (Fukunaga et al., 2019)
Surface descriptors	Surface of living coral cover by growth form (branching, encrusting, massive, tabular) and total coral cover	Square meters (m^2)	The cover of particular coral growth forms and overall living coral cover determine reef fish assemblage structure (e.g., Bell & Galzin, 1984; Kerry & Bellwood, 2012; Wilson et al., 2008). In addition, they represent, per se, indicators of coral reef status
Mapping descriptors	Abundance of coral colonies by growth form (branching, encrusting, massive, tabular) and total abundance	Number (n)	Studies of coral communities are mainly based on cover estimations (see González-Barrios & Álvarez-Filip, 2018). Simultaneously considering abundances provide information about the size of colonies and thus coral growth and demographic patterns (Hernández-Landa et al., 2020)
	Mean distance to nearest neighbor by coral growth form (branching, encrusting, massive, tabular)	Meters (m)	At the reefscape scale, connectivity between coral colonies (i.e., m to dam) influences numerous processes such as competition, predation, and microhabitat selection by reef fishes (Belmaker et al., 2009, 2011; Nanami & Nishihira, 2003). Connectivity between different growth forms likely influences different fish populations (e.g., Kerry & Bellwood, 2012; Wilson et al., 2008)
3D descriptors	Volume of shelter by coral growth form (branching, massive, tabular) or total	Cubic decimeter (dm^3)	By providing shelter of highly variable sizes (from a few mm to several dm), each growth form promotes different fish and invertebrates populations (Idjadi & Edmunds, 2006; Kerry & Bellwood, 2012; Wilson et al., 2008). For each growth form, R code is available for standardized and easy calculation of the shelter provided (Urbina-Barreto, Chiroleau, et al., 2021a)
	Shannon Shelter Index (SSI)	Index (unitless)	The diversity of shelter within a reefscape may also influence biodiversity. R code is available for its standardized and easy calculation (Urbina-Barreto, Chiroleau, et al., 2021a)

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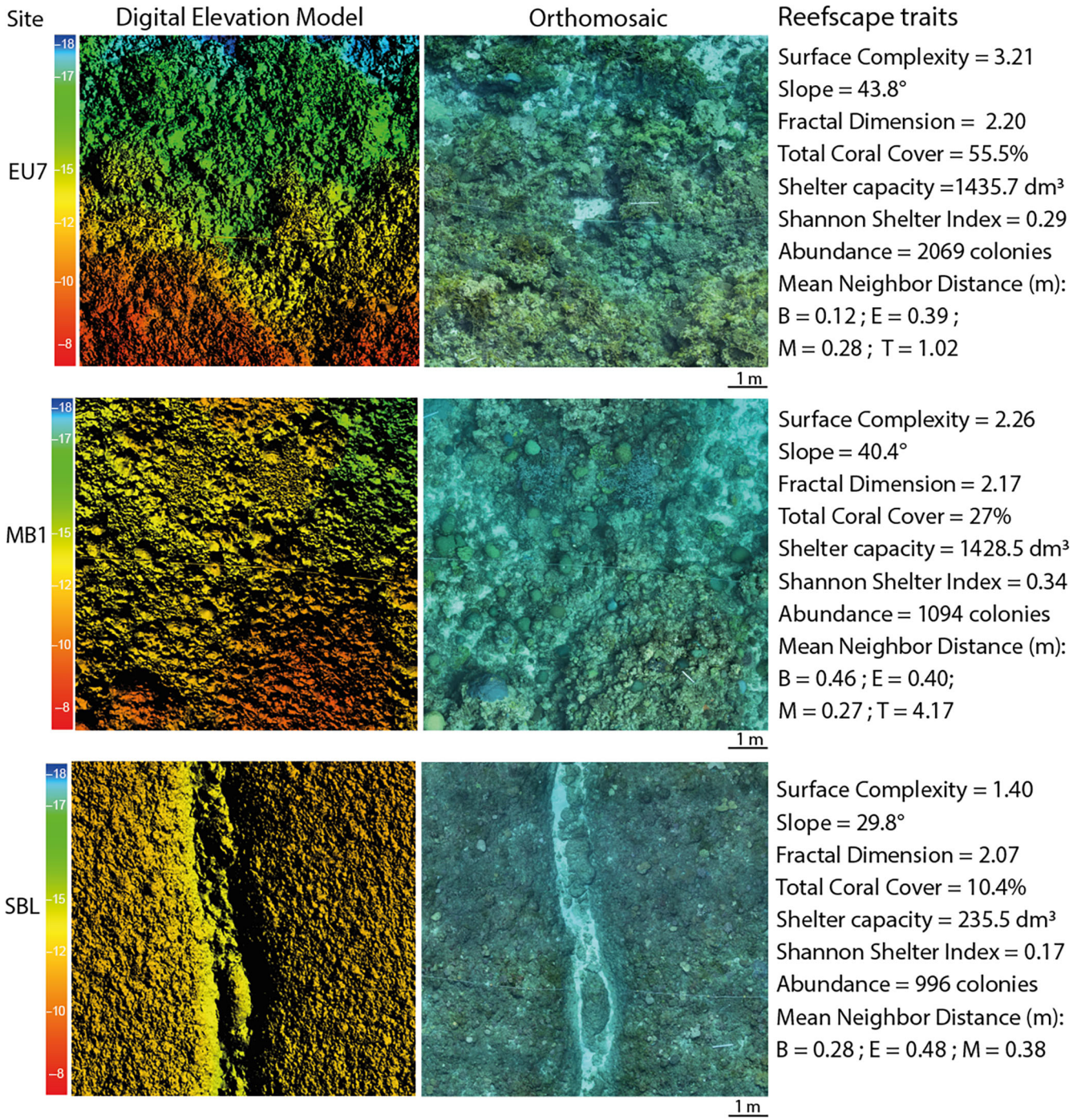

FIGURE 2 Reefscape traits at three study sites. EU7: highly complex reef (Europa); MB1: moderately complex reef (New Caledonia); and SBL: less complex reef (Reunion). An area of the digital elevation model and corresponding orthomosaic is shown for each site. B = branching, E = encrusting, M = massive, T = tabular

Surface descriptors

Planar area was computed for each delineated colony using the command *area($geometry)* in QGIS. Total coral cover and covers of branching, encrusting, tabular, and massive growth forms (i.e., the most represented forms) were calculated.

Mapping descriptors

Total abundance of branching, encrusting, tabular, and massive colonies were computed by totaling the number of corresponding polygons using QGIS. Total abundance of all coral colonies was also computed. Nearest neighbor distances were computed using the centroid

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of each polygon by measuring its distance to the centroid of the nearest polygon of similar growth form. Measurements were averaged by site and growth form (Appendix S2: Figure S1).

3D descriptors

Shelter volumes provided by branching, massive, and tabular colonies were calculated using the predictive models proposed by Urbina-Barreto, Chiroleu, et al. (2021a). The total shelter capacity was computed as the sum of all shelter volumes provided by these growth forms. A Shannon Shelter Index (SSI) was computed to reflect the diversity of shelter volumes available at each site following the expression: $\mathrm{SSI} = -\sum p_i \log(p_i)$ where p_i = the proportion of the total shelter volume provided by a given growth form.

Fish assemblage evaluation and definition of functional entities

Video footage (unbaited remote underwater stereo-video, UBRUV) was used to evaluate reef fish assemblages at Europa Island and New Caledonia sites (e.g., Myers et al., 2016; Zarco-Perello & Enríquez, 2019). Stereo-cameras (two GoPro cameras, San Mateo, USA) affixed 50 cm above the substrate filmed during 90 min an area covering approximately 150 m^2, overlapping a large proportion of the 3D modeled area. Cameras were oriented so that footage captured half substrate and half the water column above. We identified individual fish and estimated an index of abundance and biomass for each species, using the software EventMeasure (SeaGIS, Bacchus Marsh, Australia). The maximum abundance "MaxN" for a species was calculated as the maximum number of individuals of this species that can be observed on a single frame of the footage. Their size was measured, and their biomass evaluated, to calculate the maximum biomass "MaxB" of the species. The coefficients "a" and "b" which define the relationship between fish length and weight for each species were extracted from FishBase (2019).

At Reunion Island sites, reef fish assemblages were visually assessed using underwater visual census (UVC; e.g., Labrosse et al., 2002) along three 5 × 30 m belt transects deployed inside and around the 3D modeled area. During each census, a diver swam over the transect line identifying, counting, and evaluating the size of all fishes within 2.5 m on either side of the central line. Highly mobile and wary species were enumerated on the first pass as the transect line was laid and all the remaining species during the second pass. Transects encompassed the entire water column from the seafloor to surface. All detected fishes were recorded.

For each species recorded in the study, eco-morphological traits were compiled from FishBase (2019) according to the classification used in the recent literature (e.g., McLean et al., 2021). Five traits were considered (Urbina-Barreto, 2021): diet, species size class, schooling behavior, adult home range (mobility), and position in the water column. Diet was divided into six categories (HD: herbivores–detritivores; OM: omnivores; SI: sessile-invertebrate feeders; MI: mobile-invertebrate feeders; PK: plankton feeders; FC: piscivores). Species size, based on maximum total length recorded in the literature, was assigned to one of six size classes (S1: <7 cm; S2: 7–15 cm; S3: 16–30 cm; S4: 31–50 cm; S5: 51–80 cm; and S6: >80 cm). Schooling behavior was divided into solitary species (Sol), species living in pairs (Pair), species living in small groups (Small G: 3–20 fish on average in a group), medium size groups (MedG: 20–50 fish), and large groups (LargeG: >50 fish). Adult home range was divided into sedentary species (Sed), mobile species (Mob—staying within the same reef for several days), and very mobile (VMob—constantly moving around usually changing reefs within a day). Position in the water column was divided into species laying on the bottom (bottom—benthic), species hovering just above the bottom (low—demersal), and species hovering high above the reef (high—pelagic).

Functional entities (annotated "FEs") were defined as the combinations of two traits (e.g., diet-size, size schooling; see, e.g., McLean et al., 2021). The 10 possible types of trait combinations produced 195 FEs in our data set. Among them, four were selected since they gathered species known to contribute to key processes that promote coral reef functioning and fish productivity (Brandl et al., 2019; Harborne et al., 2017; Morais & Bellwood, 2019): grazers (i.e., including both scraping and grazing species described in Green & Bellwood, 2009), planktivores, predators (i.e., tertiary consumers), and preys (i.e., secondary producers) (Table 2). The number of species, the total abundance, and total biomass (non-transformed and log-transformed) were tallied within each FE for use in subsequent analyses. To homogenize the data collected by UVC along transects and by video footage sampling, these metrics were averaged among the three transects at each Reunion Island site (a single 30 m belt-transect covers a 150 m^2 surface area, equivalent to the coverage of video footage). Although this effort was made to homogenize the data, we cannot affirm that the metrics computed from UVC and video footage (e.g., abundance and MaxN) provide strictly identical results.

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TABLE 2 Key ecosystem processes and potential corresponding fish functional entities (FEs) and families

Key ecosystem process	Functional entity	Main families represented in the FE
Secondary production	Preys (Sed-Low)	Blenniidae, Chaetodontidae, Labridae, Pomacentridae, Pseudanthias sp.
Plankton assimilation	Planktivores (S3-Vmob)	Caesionidae
Herbivory–bioerosion	Grazers (HD-S4)	Acanthuridae (herbivory), Scarinae (herbivory, detrivory, and bioerosion)
Predation	Predators (S6-Sol)	Carcharhinidae, Serranidae

Notes: Codes in parentheses represent the traits shared by the species included in each FE (see Materials and Methods section and Urbina-Barreto, 2021). Preys: sedentary species low in the water column; planktivores: very mobile species measuring between 15 and 30 cm total length; grazers: herbivore–detritivore species measuring between 30 and 50 cm total length; predators: solitary species measuring more than 80 cm total length.

Statistical analyses

Spearman's rank correlations were used to explore pairwise relationships among all habitat descriptors. Four non-collinear habitat descriptors, with correlation coefficients <0.6 and variance inflation factor (VIF) values <2, were retained for subsequent analyses (Darling et al., 2017; Zuur et al., 2010).

We used linear mixed-effect models (LMMs) to explore the relationships between the diversity, abundance, and biomass of the four key fish functional entities (grazers, planktivores, predators, and preys) and the habitats descriptors selected after pairwise correlations and VIF analyses (Bolker et al., 2009; Zuur et al., 2009). We accounted for the hierarchical structure in the data and varying fish survey method between sites by including island identity (Europa, New Caledonia, or Reunion) as a random effect affecting the intercepts in the models (i.e., we allowed the means of the fish metrics to vary across islands). We conducted separate analyses for each combination of functional group (grazers, planktivores, predators, and preys) and metric (diversity, abundance, and biomass, with or without log-transformation). The most parsimonious models for describing the metrics were selected using model selection based on the small-sample corrected Akaike's information criterion (AIC_c) (Burnham & Anderson, 2002). We ran a complete set of models with all possible combinations of the fixed effects and determined the subset of "best models" as the ones with ΔAIC_c value <2. We additionally used Akaike weights derived from the AIC_c ($wAIC_c$) to evaluate the relative likelihood of each model, given the data set and the set of models considered, and to estimate the relative importance of each variable by summing these $wAIC_c$ across the models in which they were included. Akaike weights are directly interpreted in terms of each model's probability of being the best at explaining the data (Burnham & Anderson, 2002). We used R (v 4.0.4, R Core Team) and the packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) to run the LMMs.

RESULTS

Habitat descriptors

Surface complexity, fractal dimension, and mean slope were highly and positively correlated (Spearman rank $\rho > 0.9$, top-left black triangle in Figure 3), while they were weakly correlated with all other habitat descriptors ($\rho < 0.7$). Abundance of colonies, surface, and shelter capacity were positively correlated for all coral growth forms ($\rho > 0.75$; black triangles on the left of Figure 3), except for the abundance and shelter capacity of branching corals. Abundance of colonies, surface, and shelter capacity were negatively correlated to the mean distance to nearest neighbor, in particular for massive and encrusting forms. Total coral cover was highly correlated ($\rho > 0.8$) with the surface and abundance of encrusting forms. Total shelter capacity was less correlated with shelter provided by tabular colonies ($\rho = 0.67$) than with the shelter provided by branching colonies ($\rho = 0.77$). The SSI had the lowest correlations with all other habitat descriptors. Representing three groups of habitat descriptors, surface complexity, total shelter capacity, coral cover, and SSI showed low multicollinearity ($\rho < 0.6$, VIF values < 2, dashed black rectangles in Figure 3) and were retained for subsequent modeling.

Regarding differences between localities, surface complexity was significantly lower at Reunion than at Europa (Kruskal–Wallis and post hoc Dunn's tests, $p < 0.05$), while total shelter capacity was significantly lower at Reunion than at New Caledonia (Kruskal–Wallis and post hoc Dunn's tests, $p < 0.05$). Total coral cover was significantly lower at Reunion than at Europa and New Caledonia (Kruskal–Wallis and post hoc Dunn's tests, $p < 0.001$). No significant differences were detected among the three localities for SSI (Kruskal–Wallis tests, $p > 0.1$).

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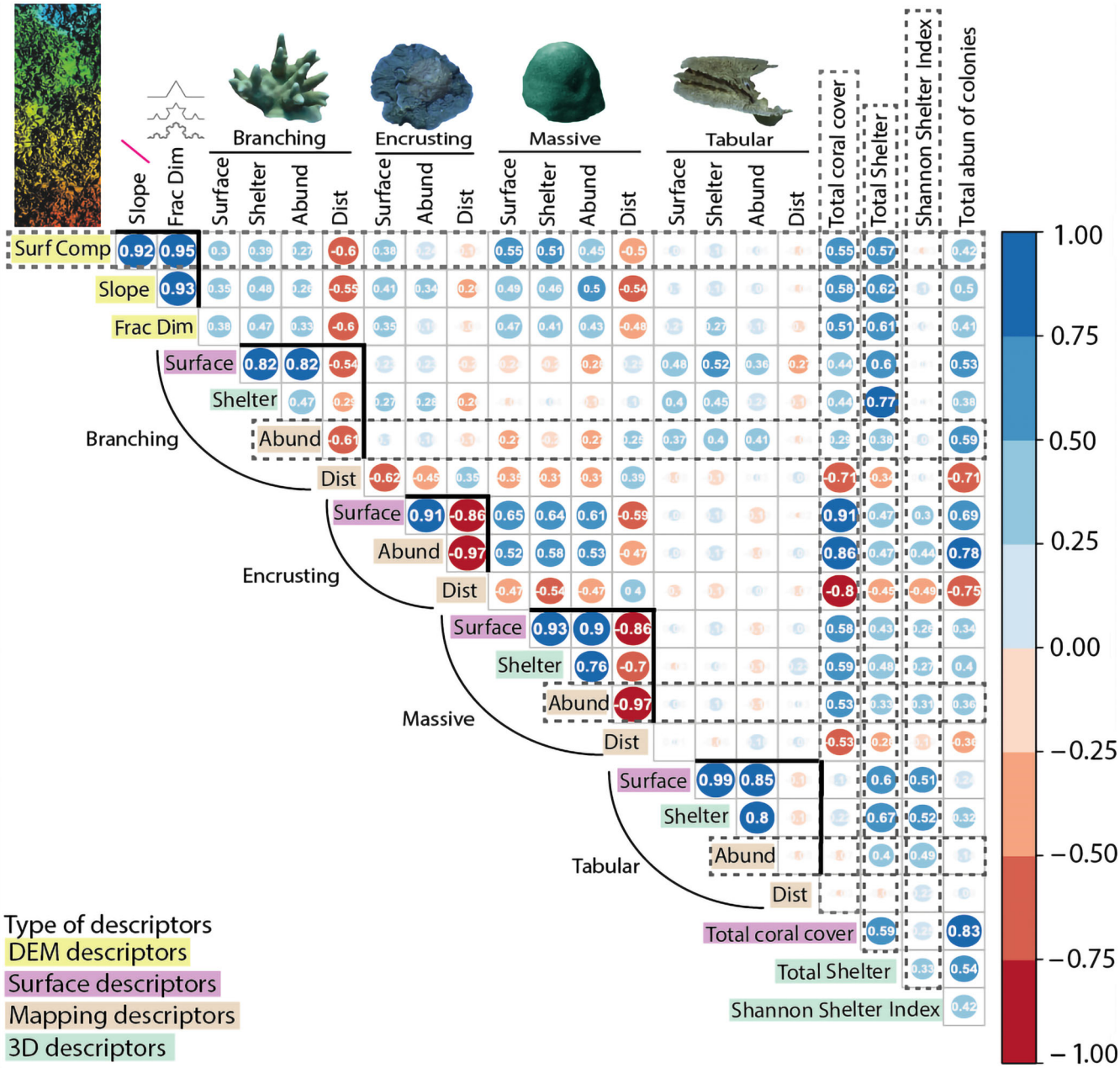

FIGURE 3 Results of Spearman's rank correlation tests among habitat descriptors. Size and color of circles represent the strength of correlation (blue for positive and red for negative). Color codes in boxes indicate the type of descriptors. Thick black lines (triangles) indicate correlations among DEM habitat descriptors and among descriptors for each growth form. Dashed rectangles show the habitat descriptors with low multicollinearity. Surf Comp = surface complexity, Frac Dim = fractal dimension, Abund = abundance of colonies, Dist = mean distance to nearest neighbor

Relationships between fish assemblages and habitat descriptors

A total of 331 fish species representing 45 families and 117 genera were recorded. The four functional entities on which we focused comprised 81 species (Urbina-Barreto, 2021). On average, these four functional entities represented 18.0% (±5.4) of site species diversity, 23.2% (±22.0) of total abundance, and 41.6% (±23.3) of total biomass.

None of the habitat descriptors explained the variance of the diversity of prey and planktivores, or the variance of the abundance of grazers and predators (the most parsimonious models in these cases were intercept-only models). For the other fish metrics, marginal R^2 ranged from 0.35 (planktivore biomass) to 0.80 (predator biomass), with a mean value of 0.47 (Table 3).

Prey abundance and biomass was explained by coral cover, SSI, and the total shelter capacity (Table 3).

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TABLE 3 Results of the linear mixed-effect models performed for predicting the diversity, abundance, and biomass of four key functional entities (preys, planktivores, grazers, predators)

Functional entity	Metric	Intercept	Fixed effects: Coral cover	Surf comp	Total shelter	SSI	p	AIC_c	Delta AIC_c	Weight	Marginal R^2
Prey	Abundance	154.8	124.4				1	334.3	0	0.336	0.215
		154.8	193.9		−96.12	−90.64	3	334.7	0.44	0.271	**0.397**
		154.8	138.3			−67.46	2	335	0.78	0.228	0.309
		154.8	159.8		−67.09		2	335.7	1.43	0.165	0.27
	Variable importance		*1*		*0.44*	*0.5*					
	Log (biomass)	6.536	1.087		−0.3733		2	71	0	0.513	**0.547**
		6.536	0.8901				1	71.1	0.11	0.487	0.39
	Variable importance		*1*		*0.51*						
Planktivores	Abundance	74.17		133.1			1	320.2	0	1	**0.418**
	Log (biomass)	4.742		2.534			1	135.6	0	1	**0.35**
Grazers	Diversity	4.33		1.162		0.79	2	97.4	0	1	**0.384**
	Log (biomass)	7.65				0.8914	1	103.5	0	0.291	0.167
		7.724	0.8444			0.7507	2	104	0.45	0.232	0.292
		7.724		0.8206		0.9011	2	104.1	0.54	0.222	0.27
		7.724	0.9994				1	105.2	0.65	0.128	0.201
		7.724	0.5874	0.5643		0.7873	3	105.2	1.65	0.127	**0.393**
	Variable importance		*0.49*	*0.35*		*0.87*					
Predators	Diversity	2.75		0.8786	0.9057		2	93.9	0	1	**0.469**
	Biomass	26,140		5711	30,990		2	534.1	0	0.563	**0.802**
		25,830			30,990		1	534.6	0.51	0.437	0.757
	Variable importance			*0.56*	*1*						

Note: For each combination of functional entity and metric (diversity, abundance, and biomass, with or without log-transformation), bold characters indicate the most explanatory model among the subset of "best models" (ΔAICc value <2).

Planktivore abundance and biomass was only explained by surface complexity. Grazer diversity was explained by surface complexity and SSI. For grazer biomass, the variance was mostly explained by SSI, while including coral cover and surface complexity in the models resulted in an equally parsimonious model (Table 3). Predator diversity was similarly explained by surface complexity and total shelter capacity. Variance of predator biomass was mostly explained by total shelter capacity, while models including surface complexity were equally parsimonious (Table 3).

Prey abundance was significantly lower at New Caledonia than at Europa (Kruskal–Wallis and post hoc Dunn's tests, $p < 0.001$). Prey biomass, grazer biomass, and predator diversity were significantly lower at Reunion than at Europa (Kruskal–Wallis and post hoc Dunn's tests, $p < 0.01$, $p < 0.05$, and $p < 0.05$, respectively). Grazer diversity and predator biomass were significantly lower at Reunion than at Europa and New Caledonia (Kruskal–Wallis and post hoc Dunn's tests, $p < 0.01$ and $p < 0.001$, respectively). Planktivore abundance and biomass were not significantly different among the three localities (Kruskal–Wallis tests, $p > 0.1$).

DISCUSSION

Hitherto, reef benthic communities, and coral reef states have often been characterized using coral cover as the main descriptor (Graham, Nash, et al., 2011; Hill & Wilkinson, 2004; Loya, 1972; Obura et al., 2019). While the importance of measuring physical descriptors of the habitat was identified early (Risk, 1972), the lack of standardized tools able to provide accurate measurements has hindered their wide adoption in monitoring programs (Graham & Nash, 2013; Hill & Wilkinson, 2004; Obura et al., 2019). Today, new tools such as underwater photogrammetry make it possible to quantify a large suite of habitat descriptors (e.g., Burns et al., 2019; Carlot et al., 2020; Figueira et al., 2015; Urbina-Barreto, Chiroleu, et al., 2021a; Zawada,

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Dornelas, et al., 2019). Identifying the redundancies and complementarities among these descriptors, and examining the role of reefscape traits in determining associated biodiversity will improve the assessment and understanding of the distribution of coral reef biodiversity and ecosystem functioning. Our results confirm the relevance of these four complementary habitat descriptors for quantifying major reefscape traits. In addition, we explore how these reefscape traits support four fish functional entities that grouped species ensuring similar key functions (or contributing to similar core processes) in the ecosystem preys, planktivores, grazers, and predators.

Habitat descriptors

All DEM descriptors (i.e., slope, fractal dimension, and surface complexity) were strongly interrelated. These findings confirm the results obtained by Fukunaga et al. (2019) who examined the redundancies among novel DEM descriptors (i.e., slope, fractal dimension, platform and profile curvature, and surface complexity) and identified fractal dimension as the most appropriate for reef benthic surveys. In contrast, correlations between DEM descriptors and other habitat descriptors were much weaker, highlighting the complementary information that they provide. For example, coral cover and surface complexity were only marginally correlated, probably because the influence of coral cover on complexity largely depends on the growth forms present (Graham & Nash, 2013; Richardson et al., 2017; González-Barrios & Álvarez-Filip, 2018; Torres-Pulliza et al., 2020); also, surface complexity can be influenced by the topography of mineral components and the underlying reef structure.

Regarding the 3D descriptors, total shelter capacity was most strongly correlated with the shelter capacities of branching and tabular colonies, suggesting branching and tabular corals are the major shelter providers (Urbina-Barreto, Chiroleu, et al., 2021a). Particularly, the case of branching colonies this strong correlation is mainly consequence of the high abundance of colonies that was the principal growth form represented in the study sites. The SSI was the least correlated with all other descriptors, underscoring that additional complementary information is provided by this descriptor. Across all morphologies, the strong correlations between shelter capacity and surface arises from shelter being calculated from the surface area of coral colonies. Nonetheless, total shelter capacity and total coral cover were less correlated due to the contribution of encrusting corals, a growth form that provides little shelter. Overall, surface area and abundance of coral colonies were highly correlated at the growth form level, whereas Hernández-Landa et al. (2020) found that this was not necessarily the case at the species level.

The mapping descriptors may offer new relevant descriptors in reefscape assessments. Indeed, colony density and their spatial arrangement indicate habitat fragmentation and spatial connectivity between colonies (i.e., habitat connectivity) at the reefscape scale, which has been shown to influence fish assemblage dynamics (Belmaker et al., 2009, 2011; Nanami & Nishihira, 2003). At a larger scale, connectivity among seascapes (e.g., Olds et al., 2012) was found to promote the resilience capacity of coral reefs (e.g., Mumby & Hastings, 2008). Future investigations considering mapping descriptors at the reefscape scale could help better explain reef species associations and distributions and improve impact assessments of natural or man-made disturbances. In addition, the evaluation of colony size frequency distributions could provide valuable information about benthic community dynamics and recruitment at different spatial scales (Adjeroud et al., 2016; Hernández-Landa et al., 2020; Jouval et al., 2019).

In their review, Tokeshi and Arakaki (2012) considered that habitat complexity was characterized by at least five traits: (1) spatial scales, (2) diversity of complexity-generating elements, (3) spatial arrangement of elements, (4) sizes of elements, and (5) abundance/density of elements. Furthermore, Torres-Pulliza et al. (2020) demonstrated that rugosity alone did not capture structural complexity on coral reefs, providing important bases for a clarification of the vocabulary employed when discussing complexity. Indeed, the various terminologies used to date, at least in coral reef studies, often do not differentiate structural complexity, habitat complexity, surface complexity, or surface rugosity. While structural complexity and habitat complexity could be considered as equivalent, surface complexity and surface rugosity only represent a part of habitat complexity. Most importantly, through their definition, Tokeshi and Arakaki (2012) clearly expressed the multifaceted nature of habitat complexity. The diversity of habitat descriptors presented in our study illustrates that underwater photogrammetry can tackle these multiple facets. Another way to reflect these complementary aspects was proposed by Fukunaga, Burns, et al. (2020) and Fukunaga, Kosaki, et al. (2020) who computed the same descriptor (i.e., vector ruggedness measure—VRM) at two different resolutions (i.e., 1 and 4 cm) to capture the complexity of branching and tabular corals, respectively. The importance of resolution when assessing habitat complexity is particularly well illustrated by Richardson et al. (2017) who used wheels of varying diameter (i.e., from 4 to 64 cm) to highlight how habitat complexity evaluation was influenced by the resolution of measurements. Underwater photogrammetry has started to integrate this multi-resolution approach (e.g., this study, Fukunaga, Burns, et al., 2020;

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Fukunaga, Kosaki, et al., 2020). Nonetheless, it will certainly be of utmost interest to go further and consider even larger panels of resolution, from a centimeter to several meters, so as to simultaneously capture the complexity ranging from small branching corals to that of spurs and grooves. This could be realized by degrading the resolution of SfM data or by using LIDAR-based data (e.g., Wedding et al., 2019).

Relationship between fish assemblage structure and habitat descriptors

Most studies examining fish–habitat relationships have identified coral cover to increase the overall diversity, abundance, and biomass of fish assemblages (e.g., Alvarez-Filip et al., 2011; Bell & Galzin, 1984; McClanahan et al., 2011). In our study, this was particularly true for the abundance and biomass of preys (i.e., sedentary small-bodied fishes such as *Pomacentridae*) that dwell among or within coral colonies of diverse growth forms (Alvarez-Filip et al., 2011; Pratchett et al., 2008; Wilson et al., 2008). Nonetheless, the best models for prey abundance and biomass included total shelter capacity and SSI, which highlights the added value of considering these new 3D descriptors in the prediction of fish assemblage structure.

While surface complexity, also named as structural or habitat complexity in former studies, has been found to be positively correlated to overall diversity, abundance, and biomass of fishes (e.g., Darling et al., 2017; Friedlander et al., 2003; Fukunaga, Kosaki, et al., 2020; Graham & Nash, 2013; Gratwicke & Speight, 2005), few studies have investigated the influence of habitat complexity on finer-grained categories of fishes (e.g., trophic groups) or predator–prey relationships (e.g., Beukers & Jones, 1997; Darling et al., 2017; Fukunaga, Kosaki, et al., 2020; Kerry & Bellwood, 2015; Kovalenko et al., 2012; Rogers et al., 2014). Here, we found that surface complexity alone explained 42% and 35% of the variance of planktivore abundance and biomass, respectively, in accordance with the findings of Darling et al. (2017) and Morais & Bellwood (2019). This result can be explained, at least in part, by the fact that the highest surface complexities were encountered, in our study as in previous ones (Darling et al., 2017; Fukunaga et al., 2019), on steep reef slopes, where the proximity to deep water promotes coastal upwelling and the advection of nutrients and zooplankton on which planktivores feed (Darling et al., 2017; Morais & Bellwood, 2019; Pinca et al., 2012).

Surface complexity was also the most important predictor of grazer diversity and was important for explaining grazer biomass. These results are consistent with the findings of Graham and Nash (2013), Darling et al. (2017), Agudo-Adriani et al. (2019), and Fukunaga, Kosaki, et al. (2020) who highlighted the positive influence of structural complexity on the abundance and biomass of Scarinae and herbivores. A novel finding of our study is the influence of SSI on grazers. Indeed, SSI was the most important predictor of grazer biomass and an important contributor to explain grazer diversity. However, understanding the mechanism underlaying how SSI influences grazer populations will require further studies with dedicated sampling designs. Coral cover was found to be important for explaining grazer biomass. This result confirms the existence of a relationship between grazers and live coral cover, while the nature of this relationship (i.e., top-down or bottom-up control) is still a matter of debate (see, e.g., Bruno et al., 2019; Robinson et al., 2018; Russ et al., 2015).

The most performant models were obtained for predator biomass. Total shelter capacity alone explained 76% of the variance in predator biomass, and the variance explained was close to 80% when surface complexity was included in the model. In addition, the variance in predator diversity was equally explained by total shelter capacity and surface complexity. As total shelter capacity mostly relies on the shelter provided by tabular and branching corals (Figure 3), these relationships could be partially explained by the provision of shelter to predators (e.g., by tabular corals; Kerry & Bellwood, 2012, 2015), to their preys (e.g., by branching corals; Wilson et al., 2008), or by a combination of both. Further investigations are needed to disentangle these effects. How shelter availability shapes the structure of fish assemblages is a fundamental question in coral reef ecology, but the lack of standardized methods to quantify shelters has made this endeavor challenging (e.g., Friedlander & Parrish, 1998; Gratwicke & Speight, 2005; Johansen et al., 2008). Our study demonstrated that photogrammetry could help to fill this gap thanks to the recently developed descriptors presented here (i.e., SSI, shelter capacity of particular growth forms, total shelter capacity; Urbina-Barreto, Chiroleu, et al., 2021a).

To summarize, the results of our models emphasized two important points. First, while coral cover is considered as an important predictor of the structure of fish assemblages, it did not contribute to the prediction of planktivore and predator metrics in our study. Second, adding surface complexity and two novel 3D descriptors in the models allowed us to explain the metrics of four key ecosystem functions ensured by fishes. This illustrates the added value of coupling fine-scale 2D and 3D descriptors to predict the metrics of key fish functions.

Limits of the study and perspectives for coral reef conservation

The three islands in the present study represent contrasted reef environments. Despite these contrasts, we found

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that the same habitat descriptors could be computed with a standardized method across all sites. It is therefore likely that the relationships between the key fish functional groups and habitat descriptors highlighted here are applicable to other coral reef areas. Indeed, by setting "island" as a random effect in our models, the three localities were considered as a random sample from a larger population (Zuur et al., 2009). However, reef fish assemblages were surveyed with a different method in Reunion, and our sampling design did not allow us to disentangle the potential effects of island and the fish survey method (i.e., the effect of island and method are confounded in the "island" random effect).

While numerous studies have evaluated the implications of using different survey methods (e.g., UVC, Baited Remote Underwater stereo-Videos, Diver Operated stereo-Videos, Rotating Videos) on the evaluation of coral reef fish assemblages (e.g., Holmes et al., 2013; Mallet et al., 2014; Schramm et al., 2020; Wilson et al., 2018), we did not find any study considering a video protocol similar to that used in the present study (i.e., 90-min video footage using UnBaited Remote Underwater stereo-Videos, UBRUV). However, in their study of tropical seagrass meadows, Zarco-Perello and Enríquez (2019) found that UVC provided lower estimations of fish diversity and abundance when compared to UBRUV. This underestimate was particularly true for herbivores and piscivores (Zarco-Perello & Enríquez, 2019). Since we used similar UVC and UBRUV protocols, our evaluation of fish assemblage structure could have been underestimated at Reunion Island. While this limitation prevents the comparison of fish metrics with the other two localities, it does not affect the validity of our models. Nonetheless, further studies integrating more localities and fish data collected with similar methods and protocols could confirm these results.

Our study has five main applications that can improve the monitoring of coral reef ecosystems.

First, maintaining ecosystem functions, including optimal levels of key fish functional entities, is increasingly recognized as a conservation priority (Bellwood et al., 2019; MacNeil et al., 2015). Thus, identifying the main reefscape traits that support these high levels is of major interest to define conservation targets. Here, the complementarity of the four 2D and 3D habitat descriptors appeared fundamental to correctly predict several key aspects of the functional structure of fish assemblages. Such trait-based approaches can support efficient conservation strategies from local to regional scales (Hoegh-Guldberg et al., 2018; Hughes et al., 2017; McLean et al., 2021; McWilliam et al., 2018).

Second, our results demonstrate that underwater photogrammetry generates new information about habitat-related factors that determine the fish assemblages, including key fish functional entities. Meanwhile, the natural variability of trophic groups metrics and productivity across environmental gradients is increasingly understood (Heenan et al., 2020; Morais & Bellwood, 2019). This newly available information could lead to comparing the actual functional structure of reef fish assemblages against what could be expected depending on local environmental specificities, so as to define achievable conservation targets. Overall, this information can significantly contribute to refining multifactorial approach studies aimed at identifying sustainable trade-offs between human exploitation and ecosystem maintenance (i.e., coral reef "bright spots"; Cinner et al., 2016).

Third, monitoring the key habitat descriptors identified in this study could also steer reef restoration actions. These could be guided by the increasing availability of image annotation solutions and 3D healthy reef models worldwide (e.g., "CoralNet"; "100 island challenge").

Fourth, our results highlight the efficiency of underwater photogrammetry for generating quantitative habitat descriptors. In fact, the monitoring of a coral reef site usually requires a 1-h dive using observer-based methods (i.e., PIT, LIT, Chain and Tape method; see Hill & Wilkinson, 2004) to collect fine-scale habitat characteristics. The data collected by underwater photogrammetry in the same time interval are standardized (i.e., no observer bias) and allow for computing multiple 2D and 3D habitat descriptors (Urbina-Barreto, Garnier, et al., 2021b). As both data collection and curation are increasingly automated, indeed, remotely operated vehicles or autonomous underwater vehicles are already used to collect data (Ferrari et al., 2016; Friedman et al., 2012; Obura et al., 2019; Price et al., 2019), and analysis solutions based on open source code (Fukunaga et al., 2019; Urbina-Barreto, Chiroleu, et al., 2021a) and artificial intelligence are increasingly being developed (e.g., González-Rivero et al., 2020; Hopkinson et al., 2020; Mohamed et al., 2020).

Finally, underwater photogrammetry offers opportunities for innovative awareness actions by generating visually attractive supports (i.e., 3D models, DEMs, orthomosaics).

To sum up, these results have several applications in fine-tuning conservation goals. We suggest the habitat descriptors: surface complexity, shelter capacity, and the Shannon Shelter Index as candidates for EOVs (Essential Ocean Variables) in reef monitoring programs (Obura et al., 2019). As conservation targets in the 21st century are numerous, and improved stewardship of coral reefs and marine ecosystems is urgent (Cinner et al., 2020; Duarte et al., 2020; Madin et al., 2019), using 21st-century technology to optimize the efficiency of coral reef monitoring programs will help to meet the challenges.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

Isabel Urbina-Barreto, Simon Elise, François Guilhaumon, J. Henrich Bruggemann, and Mehdi Adjeroud conceived the ideas; Isabel Urbina-Barreto, Romain Pinel, Simon Elise, Laurent Vigliola, J. Henrich Bruggemann, Vincent Mahamadaly, Lucie Penin, Mehdi Adjeroud, and Eric Dutrieux designed the methodology; Isabel Urbina-Barreto, Vincent Mahamadaly, Simon Elise, Laurent Vigliola, Mathilde Facon, Sophie Bureau, Christophe Peignon, J. Henrich Bruggemann, and Rémi Garnier collected the data; Isabel Urbina-Barreto, Romain Pinel, and Vincent Mahamadaly performed 3D models; Isabel Urbina-Barreto, Simon Elise, François Guilhaumon, and Gerard Mou-Tham performed data handling and analyzed the data; Isabel Urbina-Barreto, Simon Elise, J. Henrich Bruggemann, François Guilhaumon, Michel Kulbicki, Lucie Penin, and Mehdi Adjeroud led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data (Urbina-Barreto, 2021) are available from Zenodo: https://doi.org/10.5281/zenodo.5771271.

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