






## ORIGINAL RESEARCH

# Structure-from-motion photogrammetry demonstrates that fine-scale seascape heterogeneity is essential in shaping mesophotic fish assemblages

Denise J. B. Swanborn<sup>1,2,3</sup> , Paris V. Stefanoudis<sup>1,3</sup> , Veerle A. I. Huvenne<sup>4</sup> ,  
Simon J. Pittman<sup>5,6</sup>  & Lucy C. Woodall<sup>1,3</sup> 

<sup>1</sup>Department of Zoology, University of Oxford, Oxford, UK

<sup>2</sup>Department of Earth Sciences, University of Oxford, Oxford, UK

<sup>3</sup>Nekton, Oxford, UK

<sup>4</sup>Ocean BioGeosciences, National Oceanography Centre (NOC), Southampton, UK

<sup>5</sup>Oxford Seascape Ecology Lab, School of Geography and the Environment, University of Oxford, Oxford, UK

<sup>6</sup>Marine Institute, University of Plymouth, Plymouth, UK

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Habitat heterogeneity, mesophotic coral ecosystems, seascape ecology, Seychelles, SfM photogrammetry, spatial pattern metrics

## Correspondence

Denise J. B. Swanborn, Department of Zoology, University of Oxford, Oxford, UK.  
Tel: +44 1865 (2) 71234; E-mail: denise.swanborn@env-res.ox.ac.uk

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## Abstract

Benthic components of tropical mesophotic coral ecosystems (MCEs) are home to diverse fish assemblages, but the effect of multiscale spatial benthic characteristics on MCE fish is not well understood. To investigate the influence of fine-scale benthic seascape structure and broad-scale environmental characteristics on MCE fish, we surveyed fish assemblages in Seychelles at 30, 60 and 120 m depth using submersible video transects. Spatial pattern metrics from seascape ecology were applied to quantify fine-scale benthic seascape composition, configuration and terrain morphology from structure-from-motion photogrammetry and multibeam echosounder bathymetry and to explore seascape–fish associations. Hierarchical clustering using fish abundance and biomass data identified four distinct assemblages separated by the depth and geographic location, but also significantly influenced by variations in fine-scale seascape structure. Results further revealed variable responses of assemblage characteristics (fish biomass, abundance, trophic group richness, Shannon diversity) to seascape heterogeneity at different depths. Sites with steep slopes and high terrain complexity hosted higher fish abundance and biomass, with shallower fish assemblages (30–60 m) positively associated with aggregated patch mixtures of coral, rubble, sediment and macroalgae with variable patch shapes. Deeper fish assemblages (120 m) were positively associated with relief and structural complexity and local variability in the substratum and benthic cover. Our study demonstrates the potential of spatial pattern metrics quantifying benthic composition, configuration and terrain structure to delineate mesophotic fish–habitat associations. Furthermore, incorporating a finer-scale perspective proved valuable to explain the compositional patterns of MCE fish assemblages. As developments in marine surveying and monitoring of MCEs continue, we suggest that future studies incorporating spatial pattern metrics with multiscale remotely sensed data can provide insights that are both ecologically meaningful to fish and operationally relevant to conservation strategies.

## Introduction

Mesophotic coral ecosystems (MCEs), typically found in tropical and subtropical regions at water depths between 30 and 150 m (Hinderstein et al., 2010), form important fish habitats (Blyth-Skyrme et al., 2013; Lindfield et al., 2016; Rocha et al., 2018). Detailed characterisations of MCEs and their associated biodiversity remain rare compared to shallow water reefs because of the technological, logistical and financial resources required to sample and survey them (Turner et al., 2019). Knowledge of the environmental drivers and habitat preferences of MCE fish species and assemblages is fundamental to informing monitoring and sustainable management strategies (Button et al., 2021; Weijerman et al., 2019).

Benthic habitat heterogeneity is a known driver of fish assemblages across depth. Fish respond to environmental heterogeneity at multiple spatial scales, and knowledge of these patterns might therefore provide ecologically important insights (Borland et al., 2021). Conceptual tools and quantitative methods from landscape ecology can be transferred to benthic marine systems to understand the effect of multiscale benthic habitat heterogeneity. Spatial pattern metrics have been developed to quantify seascape composition (the abundance and variety of patch types), configuration (the spatial arrangement of patch types) and terrain morphology (e.g. slope, structural complexity) from habitat maps or digital bathymetric models (Lecours et al., 2016; Swanborn, Huvenne, et al., 2022; Wedding et al., 2011). In shallow water reefs, these have, amongst others, provided new insights into seascape connectivity (McMahon et al., 2012), species-specific responses to environmental structure (Hitt et al., 2011), the importance of terrain complexity (Wedding et al., 2019) and scale-dependent responses (Kendall et al., 2011). Environmental heterogeneity in seascape composition, configuration and terrain structure equally influences fishes at greater depths (Anderson et al., 2009; Moore et al., 2011).

Yet, to date, no studies have quantified multiscale benthic habitat heterogeneity using spatial pattern metrics across MCE seascapes, leaving knowledge gaps about its ecological significance to MCE fish assemblages (Swanborn, Huvenne, et al., 2022). Instead, much MCE research has focused on exploring and characterising the effect of broad-scale environmental characteristics, with water depth (Lesser et al., 2019), geographical location (Fukunaga et al., 2017; Pinheiro et al., 2016; Quimpo et al., 2019) and site geomorphology (Osuka et al., 2021) recognised as key drivers of MCE fish distribution. Furthermore, rarely are spatial pattern metrics applied to very high-resolution (cm-m) maps and models of mesophotic seascape structure, even though cm-scale metrics

quantified from models produced through structure-from-motion (SfM) photogrammetry are demonstrated predictors of shallow water and deep-sea (>200 m) coral reef fish (González-Rivero et al., 2017; Price et al., 2019).

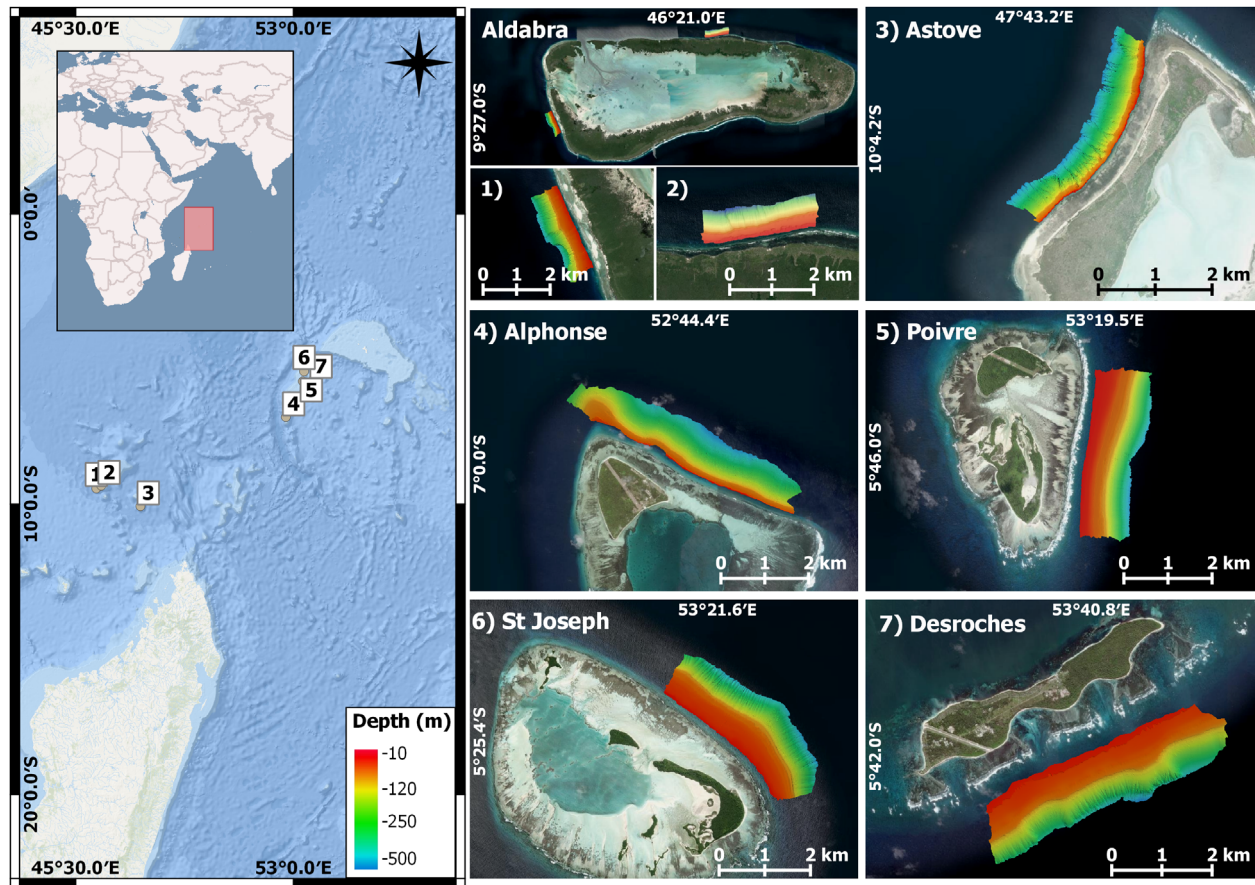
This study aims to quantify and assess the combined effect of broader scale drivers (depth, geographic location) and fine-scale (cm-m) benthic habitat heterogeneity on MCE fish assemblages by focusing on MCEs from geographically separated coral atolls in Seychelles, Western Indian Ocean. Although knowledge and interest in MCE biodiversity and conservation are increasing globally (Holstein et al., 2019; Soares et al., 2020), MCEs in the Western Indian Ocean remain particularly understudied (Pyle & Copus, 2019). Using a combination of video-based fish transect surveys and high-resolution underwater photogrammetric reconstructions of benthic seascape structure, we investigated (1) groupings of Western Indian Ocean MCE reef fish assemblages and their composition, (2) the broader scale gradients (depth and location) and fine-scale seascape characteristics (terrain structure, composition and configuration) driving those groupings and (3) their effects on assemblage characteristics within these groupings.

## Materials and Methods

Seychelles is an archipelagic state in the Western Indian Ocean. Seven research sites around six coral atolls of the Outer Islands were surveyed in March–April 2019 (Fig. 1) during the *First Descent: Seychelles* expedition (Woodall & Rivers, 2019). Aldabra, Astove, Alphonse and Desroches were located off the Amirantes Bank, although the latter was located close (16 km) to it, and St Joseph and Poivre were located on the Amirantes Bank. This study used fish and benthic data collected during submersible and remotely operated vehicle (ROV) stereo-video surveys conducted along 30, 60 and 120 m depth contours. Each survey was 250 m long, conducted with a speed of ~0.2 knots, and at a distance from the seabed of c. 1–2 m.

## Remotely sensed data

At each site, 50 m transects for photogrammetric reconstructions (Fig. 2) were extracted from the 250 m video survey's Ultra-Short Baseline (USBL) tracks. This transect length was chosen to prevent cumulative positioning errors (see Price et al., 2019) and is consistent with transect lengths used in previous Western Indian Ocean fish surveys (Osuka et al., 2018; Samoilys et al., 2019). Photo frames were extracted from downward-facing video every 2 s using FreeVideotoJPG converter (DVDVideoSoft, 2018), linked to transect USBL position using timestamps



**Figure 1.** Map of locations surveyed during First Descent: Seychelles expedition in 2019. Swath bathymetry data collected at each site between 0 and 500 m were plotted to indicate the area in which video surveys were conducted.

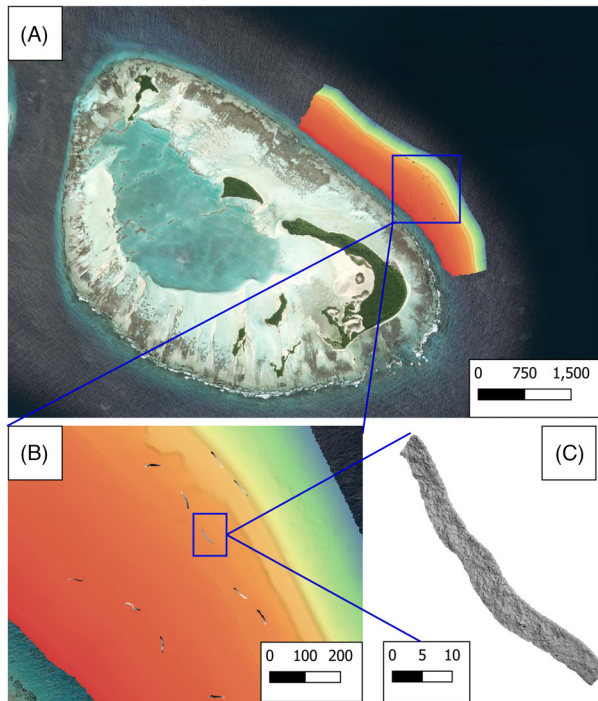
and used to construct orthomosaics and digital bathymetric models (DBMs) using SfM photogrammetry in Agisoft Metashape Professional version 1.5.5 (Agisoft LLC, 2019) (steps and settings in Appendix S1). When transects were reconstructed using data from the same 250 m video survey, they were spaced at least 25 m apart to maintain independent sampling units (Fig. 2B). SfM reconstructions were cropped to a maximum width of 5 m before constructing DBMs and orthomosaics (Fig. 3) to ensure consistency with the belt transect area used for biological data extraction (see ‘Fish assemblage data’ below), and models <40 m and >60 m long were removed to ensure consistent sampling units were used in the analysis. Although the internal, relative positioning of the 3D models was correct, owing to a lack of submersible attitude data (pitch, roll, heading), the absolute orientation of the models in space could not be determined. Hence, the resulting models were manually rotated in a horizontal plane, after which the orthomosaics and DBMs were exported at multiple resolutions, representing de-trended benthic features of multiple sizes (1, 5, 10, 15 and

20 cm), to evaluate any scale-dependent responses of fish assemblage composition to seascape structure.

### Terrain structure

Terrain derivatives measuring orientation, curvature and topographic complexity were extracted from these multi-resolution DBMs with a focal window size of  $3 \times 3$  pixels (Fig. 3B), using the R raster (Hijmans, 2017) and SpatialEco (Evans, 2017) packages (Table 1) and summarised with the mean value per transect. As the lack of attitude data prohibited the calculation of absolute slope values from the DBMs, but the slope is an important variable for mesophotic fish assemblages (Osuka et al., 2021), the mean slope value for each transect was instead calculated from bathymetric data collected by multibeam echosounder and gridded at  $2 \times 2$  m (Fig. 1, details about multibeam bathymetry data are presented in Swanborn, Fassbender, et al., 2022). Satellite data and bathymetry data (Fig. 1) were used to measure the distance to shore in QGIS 3.12.





**Figure 2.** Example of photogrammetry transect reconstructions conducted at St Joseph. (A) shows an overview picture of the site, (B) shows transect locations at the three different depths (30, 60 and 120 m) plotted on the bathymetry, and (C) represents a close-up of a transect. The scale is in metres.

### Patch metrics: composition and configuration

Multiscale orthomosaics were imported into ArcMap 10.6 for maximum likelihood classification. Per orthomosaic, 80–120 training samples representing the different substrate types (sediment (incl. Sediment veneer), bedrock, coral rubble, live scleractinian coral, macroalgae/seagrass and octocoral/sponges) evenly divided amongst classes were manually created. Four heavily shaded transects were excluded as shading compromised the tool's ability to accurately identify substrate classes. Multiscale classified files (Fig. 3C) resulting from the maximum likelihood classification were imported into FragStats version 4.2.1 (McGarigal et al., 2012) to quantify seascape composition and configuration over the entire transect (Table 1).

### Selection of predictor variables

Spearman correlation coefficients assessed the independence of predictor variables. When pairs of predictor variables were highly correlated ( $|\rho| > 0.7$ ), metrics that had the strongest correlation with total fish abundance and biomass were retained (Table 1). As spatial pattern metrics exhibited a correlation between resolutions,

Spearman correlation coefficients were calculated between multiscale spatial pattern metrics and assemblage characteristics. Only metrics at the resolution that had the strongest correlation with assemblage characteristics were retained for analysis. DBMs at 5 cm resolution were retained for terrain metrics, apart from TPI (15 cm). The patch metrics were obtained from orthomosaics extracted at 10 cm resolution. Other resolutions were removed from further analysis.

### Fish assemblage data

Fish occurrence and total length were continuously recorded using EventMeasure (SeaGIS) software (Seager, 2014) from a forward-facing survey video (Stefanoudis et al., in review). Fish were identified at the lowest taxonomic level possible and subdivided into trophic groups (Appendix S2) as a proxy for their functional role (Osuka et al., 2018; Samoilyts et al., 2019). Biomass was calculated using published length–weight relationships on FishBase (Froese & Pauly, 2020).

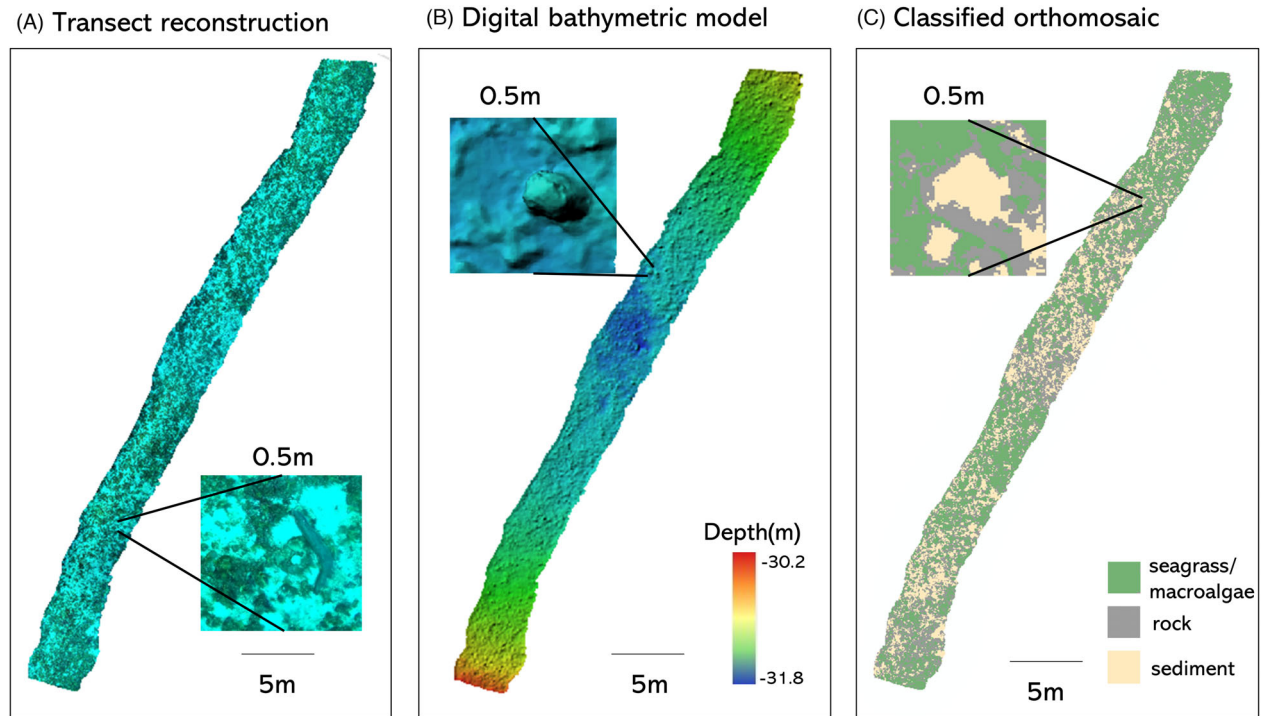
Fish observations at the locations of 50 m photogrammetric transect reconstructions were extracted from the overall 250 m video survey using time stamps. For the current analysis, three datasets were produced. The first dataset consisted of total abundance and biomass per transect. The second consisted of trophic group abundance and biomass per transect as a proxy for functional roles (Rincón-Díaz et al., 2018). The third contained transect-level descriptive data (total abundance, Shannon diversity, trophic group richness, biomass and assemblage size structure (binned fish length observations, 0–5, 5–10, 10–20, 20–30, 30–50 and >50 cm)). To enable statistical analysis, transects were excluded from the analysis when only unidentified fish were present or when fewer than three fish were observed. Unidentified fish, making up c. 4% of all observed fish, were included in abundance counts but excluded from trophic group richness, Shannon diversity and biomass counts.

### Data analysis

The final dataset contained 91 transects from the seven sites (Fig. 1) of which there were 33 from 30 m, 27 from 60 m and 31 from 120 m. All analyses were conducted in RStudio v3.5.1. For Alphonse atoll, only transects at 30 m were available, due to malfunctioning of the USBL system during transects conducted at 60 and 120 m.

### Categorising fish assemblage groupings

Ward's clustering analysis based on Bray Curtis distance on fourth-root transformed transect abundance and



**Figure 3.** Outputs of benthic data extraction, demonstrated using an example from a transect at 30 m depth at Poivre. SfM photogrammetry produced a reconstruction of a transect (A), from which a digital bathymetric model (B) and an orthomosaic were exported. The orthomosaics were classified into major substrate types present (C).

biomass data explored assemblage groupings. A univariate PERMANOVA ( $n = 9999$ ) through the ‘adonis’ function in R package *vegan* (Oksanen et al., 2018) assessed the significance of obtained groupings. A pairwise PERMANOVA elaborated on significant differences using the package *pairwiseAdonis* (Martinez Arbizu, 2020). After clustering, the composition of each grouping was assessed using trophic group proportional abundance, biomass and the proportion of individuals in each binned length class, and differences in biomass and abundance were assessed using Kruskal–Wallis tests and Wilcoxon rank-sum test pairwise comparisons. Dufrene–Legendre Indicator species analysis (Dufrene & Legendre, 1997) aimed to identify what species are significantly ( $P < 0.05$ ) associated with and characteristic of each grouping.

### Environmental drivers of assemblage groupings

Distance-based Redundancy Analysis (dbRDA) (McArdle & Anderson, 2001) established which environmental parameters and species were driving patterns in fish assemblage structure using abundance and biomass. The environmental dataset was rescaled to zero mean and unit variance before running the dbRDA and ‘site’ was included as a categorical variable. A stepwise forward

selection procedure using adjusted  $R^2$  and  $P$  values produced the most parsimonious model to explain variation in fish assemblage structure. Permutation tests ( $n = 999$ ) assessed the significance of each retained predictor variable and dbRDA axis. Associations between sites and environmental variables were visualised using biplots, where the length and direction of vectors indicate the strength and direction of the relationship, and normal confidence ordination ellipses indicated the different assemblages.

### Group-level determinants of assemblage characteristics

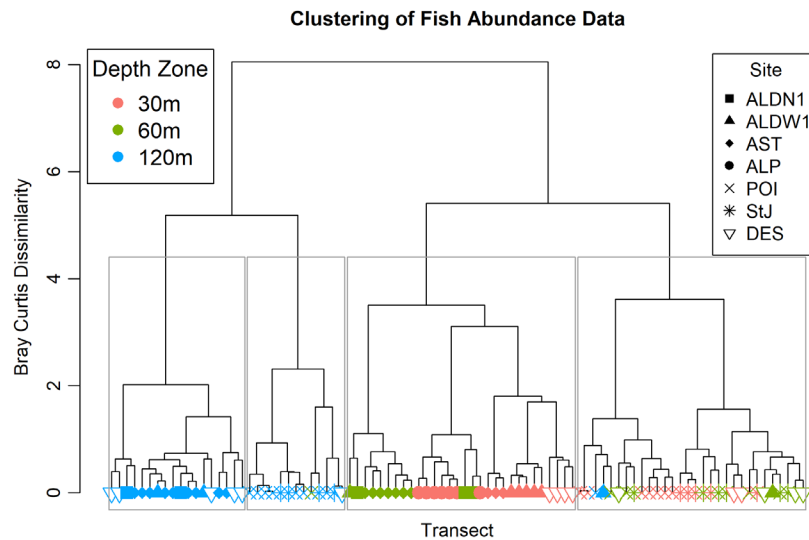
A regression-based random forest (RF) algorithm (Breiman, 2001) was applied to model the association between environmental drivers and group-level metrics (abundance, biomass, Shannon diversity, trophic group richness) per identified assemblage (referred to as ‘within-assemblage characteristics’). As clusters contained transects from multiple sites and variable depths, depth and site were included in models.

Model building, training and performance assessment was implemented using R packages *caret* (Kuhn, 2018) and *randomForest* (Liaw & Wiener, 2002). Models were

**Table 1.** Predictor variables considered for describing fish assemblage structure extracted from photogrammetric reconstructions, including metrics of continuous terrain structure, composition and configuration.

Type	Metric	Description	Retained?	Resolution retained	
Environmental gradients	Mean depth (recorded as negative values)	Average distance from seabed to surface in m	Yes (correlated with % bedrock)	m	
	Site	Surveyed atoll	Yes	NA	
	Distance to shore	Geographic proxy for cross-shelf variation in oceanographic and environmental conditions	Yes	m	
Continuous terrain structure (2.5D)	Orientation	Aspect Horn (1981) measured as eastness and northness	Yes (correlated with curvature)	5 cm	
	Topographic complexity	Vector Ruggedness Measure (VRM) Sappington et al. (2007)	Variation in the three-dimensional orientation of grid cells within a neighbourhood	Yes (correlated with TRI and SAR)	5 cm
		Topographic Roughness Index (TRI) Riley et al. (1999)	Local variation in elevation of adjacent grid cells within a neighbourhood	No (correlated with VRM)	NA
		Surface area ratio (SAR)	Ratio between the three-dimensional surface area and the planar area	No (correlated with VRM)	NA
	Curvature	Total curvature Zevenbergen and Thorne (1987)	Surface orientation and relative elevation	No (correlated with aspect)	NA
		Topographic Position Index (TPI) Weiss (2001)	Indicates whether an area is part of an elevated or depressed feature of the surrounding terrain	Yes	15 cm
	Slope	Slope (degrees) Horn (1981)	Elevational change in the terrain	Yes	2 m, from
bathymetry Patch-based metrics (2D)	Composition	Patch richness	Number of different substrates and cover types	Yes	10 cm
		Relative proportion	Percentage cover of each substrate or cover type (sediment, bedrock, coral rubble, scleractinian coral, macroalgae and seagrass)	Yes (except bedrock, which was correlated with depth and %rubble)	10 cm
		Simpson diversity Simpson (1949)	Landscape diversity as a function of proportion and richness	No (correlated with contagion and % macroalgae)	NA
		Simpson evenness Simpson (1949)	Measures how evenly dispersed substrate classes are	No (correlated with contagion and % macroalgae)	NA
	Configuration	Shape index Patton (1975)	Average shape of a substrate patch based on edge length increases with the complexity	Yes	10 cm
		Proximity index Gustafson and Parker (1992)	Unitless measure of the average nearness of a patch of the same type increases with nearness	Yes	10 cm
		Division index Jaeger (2000)	Fragmentation of the seascape, increases with subdivision	Yes	10 cm
	Contagion Li and Reynolds (1993)	Measures patch type intermixing, as well as patch spatial distribution, increases with aggregation	Yes (correlated with diversity and evenness)	10 cm	

Metrics were examined at multiple resolutions. The right column shows variables retained for analysis and at what resolution.



**Figure 4.** Clustering of fish abundance per transect where grey boxes delineate different clusters. Colours represent depth classes of observations. Symbols represent the site, with closed symbols representing off-bank islands (Aldabra, Astove and Alphonse) and open symbols representing sites on and next to the Amirantes bank (Poivre, St Joseph and Desroches).

constructed using three repeats of 5-fold cross-validation to reduce overfitting. The number of trees and variables used for splitting at each node was optimised using the RMSE (root mean square error). Ten resamples of the final model were created for performance assessment using the mean and standard errors of  $R^2$  and normalised MAE (Mean Absolute Error). Predictor variable contributions to the final random forest model are defined as the decrease in node impurity by splitting that variable, measured by the residual sum of squares, and scaled to a percentage. Partial dependence plots were interpreted to better understand the dependence between the response variables and the five most influential predictors.

## Results

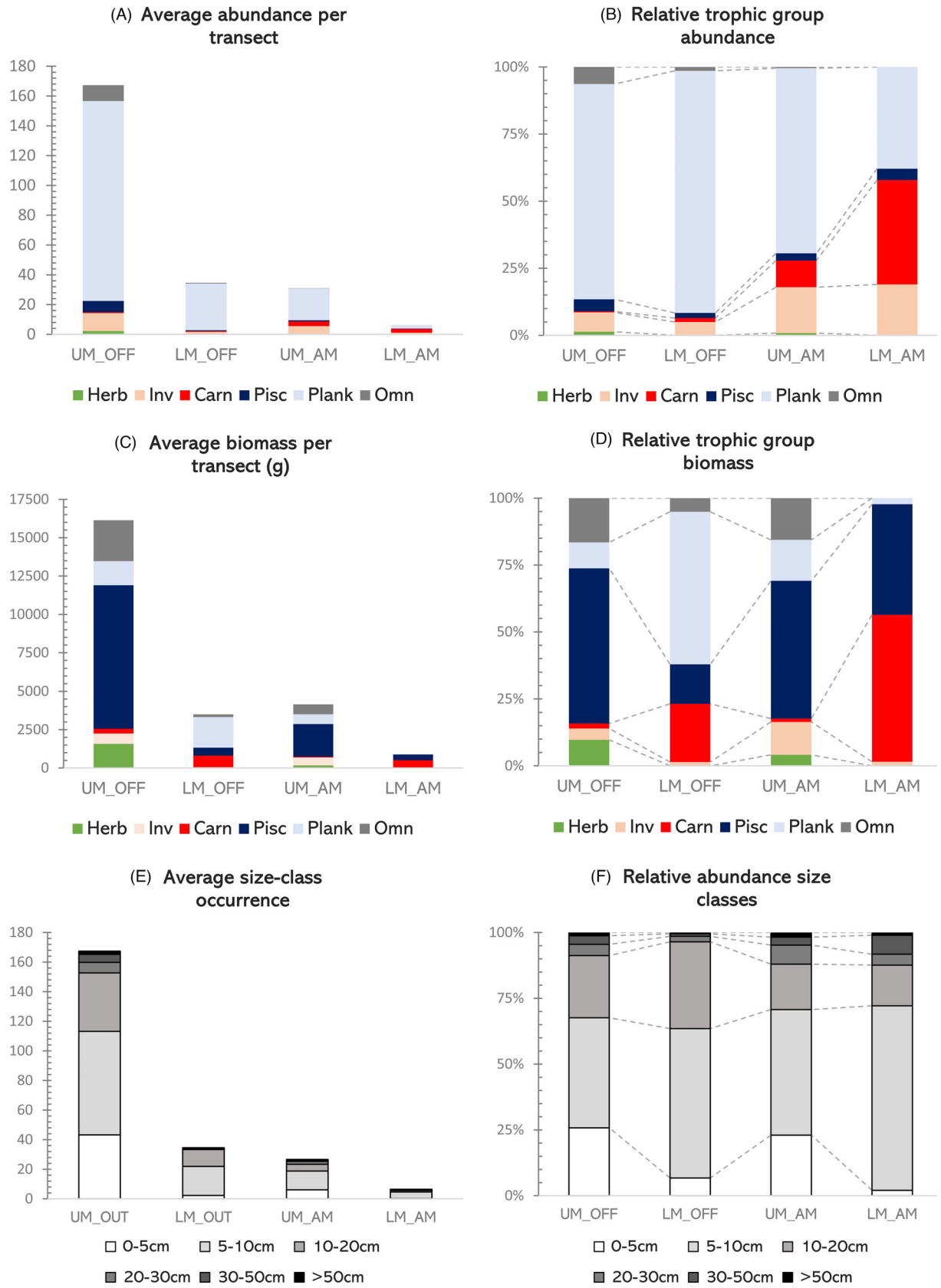
### Assemblage groupings

The clustering analysis on transect fish abundance and biomass data revealed four distinct depth- and site-driven groupings (Fig. 4; Appendix S3). The PERMANOVA confirmed significant differences between groupings ( $P < 0.001$ ), and subsequent pairwise comparisons indicated that all assemblage groupings differed from each other ( $P < 0.05$ ).

The abundance observations (Fig. 4) split into two depth-driven groups as follows: the 120 m transects and a combination of the 30 and 60 m transects. Observations clustered by site within these depth groups, with islands on the Amirantes Bank (Poivre, St. Joseph) distinct from Aldabra, Astove and Alphonse (hereafter referred to as

‘off-bank islands’). Transects at Desroches occurred across all clusters. Consequently, four assemblage clusters were delineated, representing the 30 and 60 m (‘upper mesophotic’, UM) observations of the off-bank islands (UM\_OFF), the 120 m (‘lower mesophotic’, LM) observations of the off-bank islands (LM\_OFF), the 30 and 60 m observations of the Amirantes bank (UM\_AM) and the 120 m observations of the Amirantes bank (LM\_AM). Clustering performed using biomass data found similar depth- and site-driven groupings (Appendix S3).

Subsequent assemblage characteristic comparisons provided further insight into the compositional differences between identified clusters (Fig. 5). Fish biomass per transect, but not abundance, was significantly ( $P < 0.05$ ) higher in the 30–60 m clusters than in deeper 120 m clusters at the same location. Moreover, both abundance and biomass were significantly ( $P < 0.05$ ) higher in UM\_OFF than in UM\_AM, but only biomass was higher in LM\_OFF compared to LM\_AM. In terms of trophic composition (Fig. 5A and B), planktivorous and invertivorous fish were numerically dominant across all clusters. However, the importance of planktivorous fish was reduced and replaced by higher contributions of piscivorous, carnivorous and omnivorous species when biomass data were used (Fig. 5C and D). This is reflected in the size distribution of fish with proportionately more large-bodied fish (>20 cm), that tend to be piscivorous or carnivorous, found in off-bank island clusters and a higher number of smaller individuals, typically planktivorous, dominating in shallower clusters (Fig. 5E and F).





**Figure 5.** Composition of trophic groups in each of the four identified clusters, where UM\_OFF and LM\_OFF represent the 30–60 m observations, and 120 m observations of off-bank islands and UM\_AM and LM\_AM represent the 30–60 m observations and 120 m observations of the Amirantes bank. Upper panels show average group abundance per cluster (A) and the relative abundance of trophic groups per cluster (B). Middle panels show average group biomass per cluster (C) and the relative biomass of trophic groups per cluster (D). Bottom panels show the occurrence of size classes per cluster (E) and the relative abundance of size classes (F).

Indicator species analysis revealed that 36 of the 76 species sampled were significantly associated with a specific cluster (Appendix S4). UM\_OFF was the most species-rich, containing planktivores, piscivores, invertivores and herbivores, including species of commercial interest (e.g. *Caranx* spp., *Epinephelus* spp., *Lutjanus* spp., *Cephalopholis* spp). UM\_AM showed associations with several piscivorous and invertivorous species, but few were significant. Lower mesophotic assemblages in both geographies were associated with distinct planktivorous and carnivorous fish species (e.g. *Pseudanthias* spp., *Scorpaenodes* spp.), with a higher number of planktivorous species associated with LM\_OFF.

### Drivers of assemblage groupings

In addition to broad-scale environmental drivers (depth and site) already identified (Fig. 4), fine-scale spatial terrain metrics describing habitat composition (substratum type), configuration (proximity index, contagion) and terrain structure (slope, VRM) were also statistically significant in explaining variation in assemblage abundance and biomass. Adjusted  $R^2$  values showed that 46.9% and 39.7% of the variation in abundance-based and biomass-based fish datasets, respectively, could be attributed to the combined effects of broad-scale and fine-scale environmental variables included in the model.

The final selected models contained identical predictor variables for both datasets (abundance and biomass), with the additional inclusion of contagion, rubble and scleractinian coral cover in the abundance model, and distance to shore in the biomass model (Table 2). Permutational tests ( $n = 999$ ) showed the significance of included variables (Table 2A). Depth and site were the largest contributors in both models, jointly explaining >35% of the total variation.

### Environmental influences

The ordination biplots displayed transect dissimilarity along the first and second dbRDA axes for both fish abundance (Fig. 6A) and biomass data (Fig. 6B). Environmental scores indicated which environmental variables each significant dbRDA axis represented (Appendix S5; Fig. 6). The first axis contained depth and slope, representing the shallow to deep gradient and transition from gently to steeper sloping environments. The second axis,

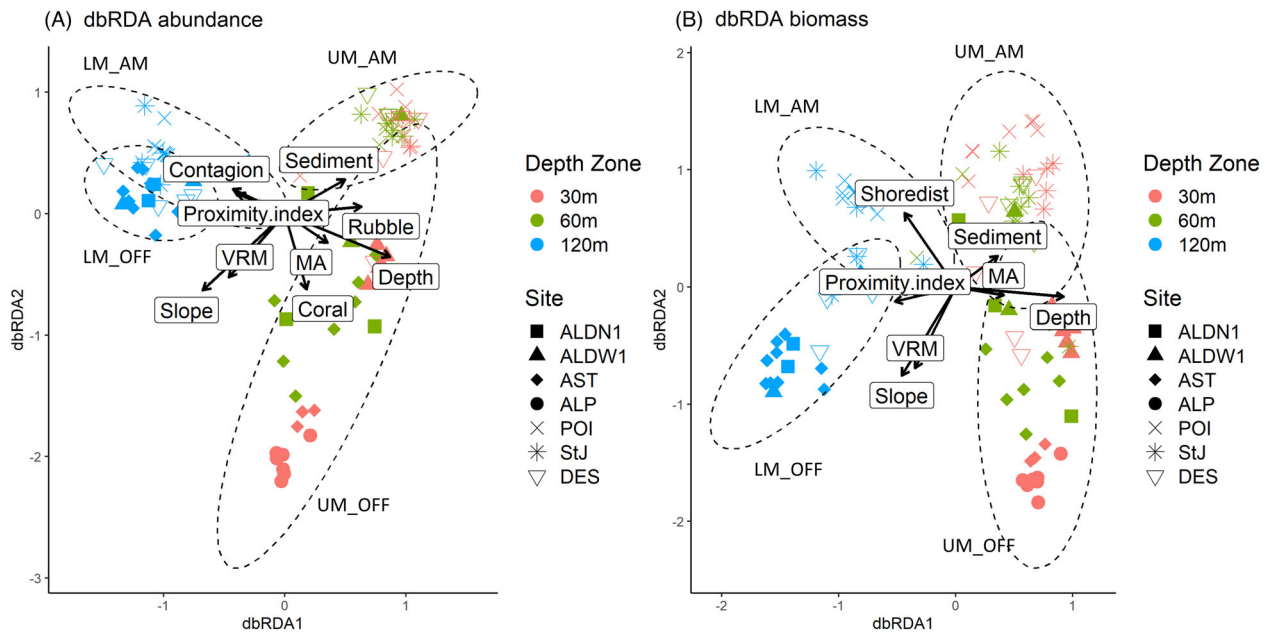
**Table 2.** Variables included in abundance (a) and biomass (b) dbRDA.

	d.f.	Sum of squares	% total unadjusted variance explained	P value
<b>(a) ANOVA</b>				
abundance dbRDA				
Site*	6	8.987	24.13	<0.001
Depth*	1	5.295	14.22	<0.001
Vector	1	1.5324	4.11	<0.001
Ruggedness measure*				
Coral*	1	1.1785	3.16	<0.001
Sediment*	1	0.8818	2.37	<0.001
Macroalgae/seagrass*	1	0.8243	2.21	<0.001
Proximity index*	1	0.7399	1.99	0.004
Slope*	1	0.5421	1.46	0.005
Rubble*	1	0.3973	1.07	0.033
Contagion	1	0.3892	1.05	0.051
Residual	75	16.475	55.76%	
<b>(b) ANOVA</b>				
biomass dbRDA				
Site*	6	8.675	23.81	<0.001
Depth*	1	4.3784	12.02	<0.001
Vector	1	1.5089	4.14	<0.001
Ruggedness measure*				
Macroalgae/seagrass*	1	1.1707	3.21	<0.001
Sediment*	1	1.0414	2.86	<0.001
Proximity index*	1	0.7629	2.09	0.002
Slope*	1	0.5809	1.59	<0.001
Shoredist*	1	0.4893	1.34	0.012
Residual variance	77	19.8226	54.40%	

\*Indicate a significant contribution to the variable.

comprising coral, VRM, slope and distance to shore, represented the gradient from structurally complex reef habitats near shore to more gently sloping environments further offshore, with site-specific gradations.

Transects were strongly separated by depth, proximity index and contagion (abundance only), with transects on the Amirantes bank (St. Joseph, Poivre) distinct from Aldabra, Astove and Alphonse across gradients of structural complexity (VRM), slope and the proportion of sediment. UM\_OFF was found on sloping and complex



**Figure 6.** Ordination biplot of species abundance (A) and biomass (B) per transect as a function of dbRDA1 (17.72% variance abundance and 14.37% biomass) and dbRDA2 (10.94% variance abundance and 9.68% biomass). Point colours show the depth zones of transects, while point shapes show the site at which each transect was conducted. Continuous environmental variables included in the model have been superimposed as vectors displaying the strength (represented by vector length) and direction of their effect, with depth included as a negative variable. The site was included as a categorical variable. Ordination ellipses indicate identified assemblage clusters.

terrain characterised by macroalgae/seagrass and live coral. LM\_OFF was found on the terrain of similar structure, but on a more homogeneous substrate environment composed mainly of bedrock (associated with depth, Table 1). UM\_AM was associated with less gradually sloping flats with sediment and coral rubble cover. Similar to LM\_OFF, LM\_AM was associated with homogeneous bedrock terrain (correlated with depth) of comparatively lower structural complexity and further from shore. The contribution of substratum types (coral, macroalgae/seagrass, sediment and rubble) was larger for abundance than for biomass (only sediment and macroalgae/seagrass) and spread was larger for biomass.

## Group-level drivers of assemblage characteristics

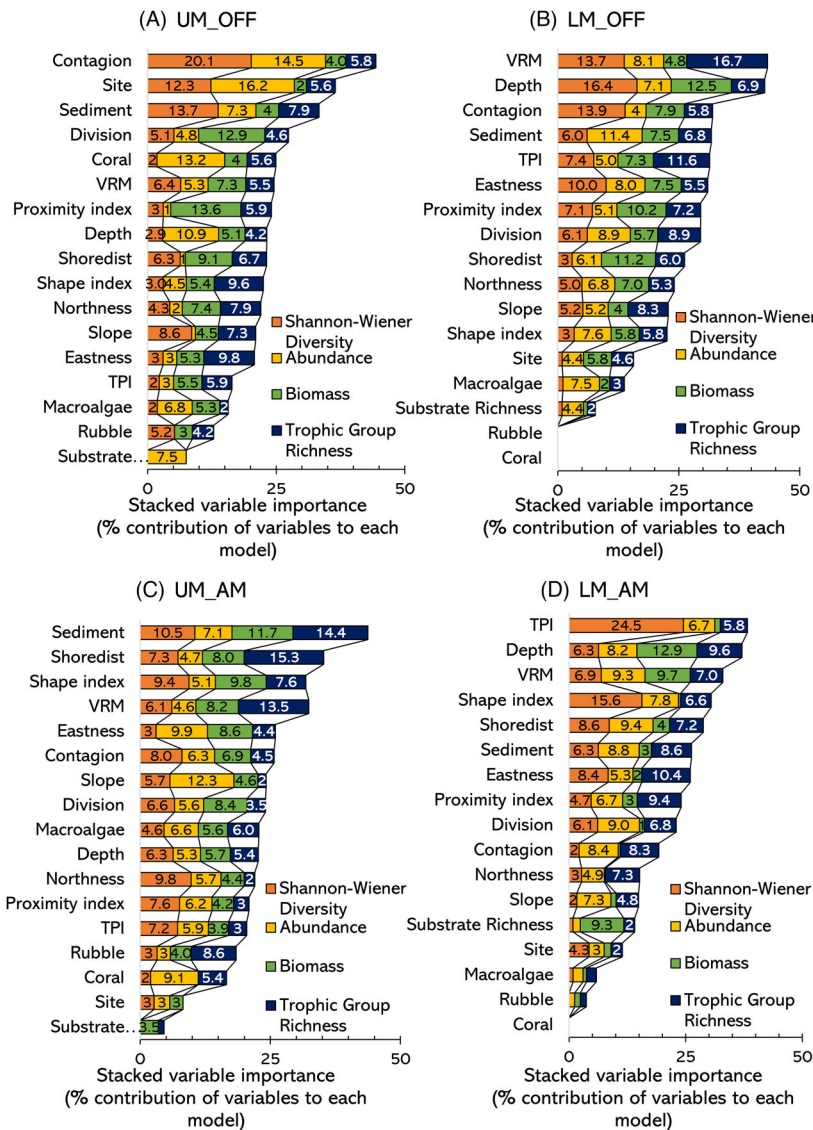
### Model performance

Constructed RF models for fish assemblage structure (abundance, biomass, trophic group richness, Shannon diversity) as a function of benthic seascape characteristics explained a good but variable proportion of variance (mean 0.62, SD 0.07) (Appendix S6). MAE values (Appendix S6B–E) showed that predictive accuracy varied between variable and grouping. Mean normalised MAE

was highest for abundance models (60.99%) and biomass models (65.29%) and shallow clusters (UM\_OFF = 50.56% and UM\_AM (62.41%)). Model performance based on benthic seascape characteristics was considered adequate as in similar shallow reef studies (Costa et al., 2014; Pittman et al., 2009), fish assemblages are also driven by the conditions of the overlying water column and wider benthic environment, which this study did not quantify.

### Variable importance

Variable importance plots (Fig. 7) revealed that final models were composed of combinations of predictor variables, with no clear patterns across assemblage characteristics. Partial dependence plots (Appendix S7) showed the effects of the five most important variables on assemblage characteristics. Within UM\_OFF (Fig. 6A, Appendix S7-1), composition metrics positively influenced abundance (coral), Shannon diversity and trophic group richness (sediment), and configuration metrics revealed more aggregated patch characteristics (contagion, proximity index) were associated with higher abundance, biomass and Shannon diversity. In the other 30–60 m grouping, UM\_AM (Fig. 6C, Appendix S7-3), composition metrics



**Figure 7.** Variable contributions to model assemblage characteristics for the shallower assemblage of the off-bank islands (UM\_OFF) (A), the deeper assemblage of the off-bank islands (LM\_OFF) (B), the shallower assemblage of the Amirantes bank (UM\_AM) (C) and the deeper assemblage of the Amirantes bank (LM\_AM) (D). Variable contributions were standardised to a percentage of the overall assemblage descriptor model and stacked to evaluate variable importance across models.

equally showed positive effects of patch types on abundance (coral), biomass and Shannon diversity (sediment), and trophic group richness (rubble), while configuration metrics showed a positive relationship between complex patch shapes and Shannon diversity and richness. In both 120 m groupings (Fig. 6B and D, Appendix S7-2,4), structurally complex (high VRM) and elevated terrain (TPI) measured using terrain metrics drove fish abundance, Shannon diversity and trophic group richness. Additionally, fine-scale fragmentation (high division index, high proximity index, reduced contagion)

positively influenced abundance, Shannon diversity and trophic group richness at LM\_OFF, but effects of composition and configuration were less clear at LM\_AM.

### Discussion

Understanding the multiscale environmental drivers of MCE fish assemblages is important to understand their ecology and functioning, and thus aid their conservation and management. Using the Seychelles atolls as a study system, this study revealed that

broad-scale drivers of depth and location shape distinct grouping of mesophotic fish assemblages, and that these groupings exhibit variable responses to fine-scale terrain structure, seascape composition and configuration at mesophotic depths (30, 60 and 120 m). The findings highlight a need to develop research and monitoring programmes explicitly incorporating environmental data across spatial scales to improve insights into the ecological effect of mesophotic habitat heterogeneity.

## Mesophotic fish–habitat associations

### Broad-scale assemblage groupings

Assemblages were separated along gradients of depth, site and geomorphology.

Depth-dependent shifts in MCE fish abundance, biomass and taxonomic composition concur with previously reported effects of depth (Andradi-Brown et al., 2016; Kahng et al., 2014; Stefanoudis et al., 2019). The taxonomic distinctiveness of the 120 m assemblages from those at 30 and 60 m follows findings elsewhere (Button et al., 2021; Pinheiro et al., 2016) and might indicate a faunal break between these depths (Lesser et al., 2019). However, there was a lack of data between 60 and 120 m and therefore the transition of fish assemblages may also be gradual. Changes in the relative abundance and biomass of trophic groups with depth match those previously discussed in literature in other regions (Andradi-Brown et al., 2016; Kahng et al., 2010; Stefanoudis et al., 2019).

Fish assemblages vary across geographic locations because of regional differences in environmental conditions, connectivity and historical use patterns (e.g. fishing activity) (Samoilys et al., 2019). Regional differences in Western Indian Ocean oceanographic conditions mediated by the African mainland and the Mascarene Plateau (Obura, 2012) influence biogeography (McClanahan et al., 2014), likely resulting in compositional differences between the eastern and western sites. Study sites also differ in local geological settings (Fig. 1), particularly their distance to the Amirantes Bank (Mart, 1988). Sites on the Amirantes Bank (Poivre, St. Joseph) have different exposure to local circulation than sites off it (Aldabra, Astove, Alphonse, Desroches) (Hamylton et al., 2012). Desroches is off the Amirantes bank yet close (16 km) to it, which may explain the shared ecological characteristics with both Amirantes and off-bank sites. Further, geographic location may act as a proxy for historical use and protection. The lower abundance and biomass of commercially important omnivorous and piscivorous species (Lutjanidae, Lethrinidae, Carangidae, Serranidae) at the Amirantes sites compared to the off-bank islands is consistent

with historical artisanal and subsistence fishing patterns, that traditionally dominated coastal domestic catch (Christ et al., 2020). Although Aldabra has also been afforded long-term marine protection, it is difficult to determine the absolute effect without appropriate baselines.

Furthermore, local site geomorphology differed between survey sites in the off-bank islands and sites on and next to the Amirantes bank. Amirantes sites featured extended gradually sloping sandy shelves, whereas the off-bank sites featured short reef ridges and steep slopes (captured in this study by slope and VRM). The slope is an important predictor of MCE fish biomass (Weijerman et al., 2019) and can influence hydrographic parameters that influence the dispersion of food particles such as upwelling (Osuka et al., 2021; Sherman et al., 2019), matching the higher abundance and biomass of planktivorous and piscivorous species found in the off-bank islands. Geomorphology also influences sediment dynamics (Sherman et al., 2016), and the Amirantes sites with lower slope gradients and rugosity sites featured higher sedimentation. This inhibits coral recruitment and growth (Smith et al., 2019) and is consistent with the lower abundance/biomass of reef-dependent fish.

### Local assemblage structuring

Fine-scale variations in terrain structure, composition and configuration explained a substantial amount of variation in addition to the broad-scale drivers, especially given that fish assemblages are strongly driven by characteristics of the overlying water column.

Of the metrics describing terrain structure, fine-scale habitat complexity measured by VRM mainly influenced MCE fish, supporting results from other reef systems (Ferrari et al., 2016; Price et al., 2019). In the 30–60 m region, increased habitat complexity was linked to complex site geomorphology or hard coral in UM\_OFF. In the 120 m assemblages, habitat complexity and TPI drove abundance, trophic group richness and Shannon-Wiener diversity, demonstrating that elevated, ridge-like features are important in supporting biodiverse assemblages. This is congruent with the lower mesophotic and subphotic habitat preferences previously reported in Hawaii (Weijerman et al., 2019).

Seascape composition was measured as the relative abundance of patch types and distinct substrates were associated with 30–60 m (sediment, coral, rubble and macroalgae) and 120 m (bedrock and sediment) mesophotic assemblages. The effects of coral and coral rubble on 30–60 m assemblage structure match reports of coral cover as key drivers of MCE assemblages (Quimpo et al., 2019), whereas the proportion of sediment



supported trophic group richness, Shannon-Wiener diversity and biomass. The proportion of sediment also positively influenced LM\_OFF mesophotic fish abundance in the otherwise homogeneous bedrock environment at 120 m. Previous shallow reef studies found that as fishes use multiple environments, patch mixtures including sediment can positively influence fish assemblages (Sievers et al., 2020). These results indicate that these effects extend into deeper reef systems.

Configuration metrics measured the spatial arrangements of patch types. At UM\_OFF, assemblage abundance and biomass increased with more aggregated and connected seascape characteristics. Aggregation could indicate structural connectivity, which has proven important in maintaining fish abundance and biomass in shallow water coral reefs (Grober-Dunsmore et al., 2007). Additionally, diversity and trophic group richness at UM\_AM increased with complex patch structure, indicating that fine-scale spatial heterogeneity is important in maintaining diverse assemblages (Hewitt et al., 2005). In the lower mesophotic clusters, fine-scale fragmentation appeared to support fish abundance, functional group richness and Shannon diversity. This may reflect the patchiness of mesophotic benthic cover (octocorals and sponges) and sediment at 120 m, which tend to form more isolated patches on and between bedrock that are nevertheless beneficial for the resident fish fauna, whereas at 30–60 m ecologically important benthic cover and substratum patches tend to be more extended and well connected.

### Methodological considerations

Although logistical challenges of obtaining MCE video surveys through underwater vehicles or technical diving remain, our ability to obtain high-resolution environmental and biological data beyond conventional SCUBA depth continues to increase. This study extended landscape ecology approaches developed on land and increasingly applied in shallow water environments to fine-scale remotely sensed data on MCEs. Spatial pattern metrics captured diverse aspects of seascape structure (composition, configuration and terrain structure) from SfM photogrammetry outputs to assess fine-scale (cm-m) MCE fish–habitat associations. Our findings indicate for the first time that fine-scale spatial pattern metrics explain mesophotic fish assemblage structure and habitat associations in addition to broad-scale drivers of depth and location. Outcomes also suggest the potential of this approach for similar research in other reef systems.

Although terrain metrics such as those employed here may act as a proxy for local hydrographic conditions (Wilson et al., 2007), uncaptured variations in the overlying water column (e.g. currents, primary productivity, or

water chemistry) likely contribute to the unexplained variation and imperfect predictive power of Random Forest models. Developing and incorporating pelagic metrics of seascape structure remains an important focal point for seascape studies, particularly for deeper benthic systems (Kavanaugh et al., 2016; Swanborn, Huvenne, et al., 2022).

Additionally, seascape structure influences fish assemblages at multiple scales (Anderson et al., 2009; Pittman & Brown, 2011), including scales other than the cm-scale metrics captured in this study (Weijerman et al., 2019). Although home ranges of smaller fish might be within the spatial scale covered in this study, larger-bodied fish will have home ranges that greatly exceed the 50m x 50m areas covered here, which might compromise the detection of accurate habitat relationships (Kendall et al., 2011). Further research investigating the influence of seascape structure around transects, for example derived from habitat maps, could provide key insights into the effects of the large-scale context and potential connectivity between habitats.

### MCE monitoring and conservation

At present, few conservation and management efforts directly target deep reef habitats, despite their importance for ecosystem function and services (Soares et al., 2020). Areas of high MCE fish abundance and biomass include sites with steep slopes and high terrain complexity, with upper and middle mesophotic habitats characterised by the coral cover and connected patch mixtures, and lower mesophotic habitats with fine-scale habitat heterogeneity in topography and substratum types. These areas should form important targets for future surveying and monitoring efforts as well as for fisheries. Monitoring programmes could benefit from incorporating spatial pattern metrics to identify where and when they change and to evaluate possible implications for associated species and habitats (Wedding et al., 2011). All findings on habitat associations of MCE fish at different depth zones uncovered in this study were shared with stakeholders from the region.

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## Authors' Contributions

DS conceptualised the study, conducted all statistical analyses and wrote the paper. PS calibrated, analysed and annotated the fish video data. LW created the video transect survey plan and ran the expedition. All authors contributed critically to the drafts and gave final approval for publication.

## Conflict of Interest

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

## Data Availability Statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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## Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1** Photogrammetric reconstruction parameters.

**Appendix S2.** Trophic groupings.

**Appendix S3.** Biomass plots.

**Appendix S4.** Species associated with each cluster.

**Appendix S5.** Significance of dBRDA axes and contributing variables.

**Appendix S6.** Model performance.

**Appendix S7.** Partial dependence plots.