Linking deep seabed structure to biodiversity: an exploration of seamounts and deeper reefs in the South and Western Indian Ocean



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Ithaka gave you the marvelous journey.
Without her you wouldn't have set out.

– Excerpt from *Ithaka* by C.P. Cavafy

Declaration

I declare that the work presented in this thesis is my own, conducted under the supervision of Professor Lucy Woodall (University of Oxford and Nekton), Dr. ir. Veerle Huvenne (National Oceanography Centre, Southampton), Dr. Simon Pittman (University of Plymouth and Oxford) and Professor Anthony Watts (University of Oxford). This thesis is submitted in fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Oxford. None of the work included in this thesis has been submitted, in whole or in part, for any previous degree or qualification in this University or elsewhere.

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Formatting Statement

This thesis is presented as an integrated format, where the literature review and each data chapter have been prepared as manuscripts and have been accepted for publication or are in review. I lead-authored all publications resulting from the four data chapters and the literature review in this thesis, and have acknowledged the contributions of all co-authors using CRediT taxonomy in the authors contributions section of each chapter.

The word count of this thesis (exclusive of references and bibliography, tables of contents, appendices, figures, tables and their captions) is 44,635.

COVID-19 Impact Statement

This thesis planned to draw on data collected on deeper reef ecosystems by two sea-going expeditions in 2019 (2 chapters) and 2020 (2 chapters). However, as the 2020 expedition was cancelled as a result of the pandemic, this original plan unexpectedly changed midway through the thesis. Instead of collecting field data, existing but unpublished data sets from a previous expedition on seamounts in the region were used. As this expedition focused on seamounts, the thesis was revised to consider environmental heterogeneity in both seamounts (2 chapters) and mesophotic and rariphotic reefs (2 chapters).

Abstract

Environmental heterogeneity, understood as spatial or temporal variability in environmental conditions, influences biodiversity and ecosystem processes over multiple scales, including at the deep seabed. However, as a result of the inaccessibility of the ocean beyond conventional SCUBA depth (> 30 m), key knowledge gaps remain on the biotic and abiotic patterns that influence the occurrence and distribution of seabed-associated taxa, habitats and resulting ecological processes and ecosystem services. Although seabed and habitat mapping documents seabed environmental and habitat heterogeneity, very little research explicitly quantifies it to draw conclusions on its ecological consequences. To study the character and effect of environmental heterogeneity on biodiversity and marine ecological processes in the deep sea, this thesis explored the potential of combining existing seabed and habitat mapping practices with the theoretical framework and analytical techniques from land- and seascape ecology.

This thesis first reviews seascape ecology and its potential to study the ecological implications of environmental heterogeneity at the deep seabed, and identifies theoretical focal areas for the application of tools and concepts from seascape ecology deeper than 30 m (Chapter 1: Introduction). The objectives of this thesis, based on these focal areas, can be divided in three main themes: 1) characterising spatial heterogeneity using spatial pattern metrics; 2) assessing the ecological relevance of spatial heterogeneity quantified using spatial pattern metrics; and 3) applying this knowledge to inform environmental management. Objectives are addressed through a set of case studies that provide the opportunity to explore the multi-scale relationship between seabed structure and ecology in habitats at seamounts (km-m scale, Chapter 2 and 3) and reefs found between 30 m-250 m on atoll slopes (m-cm scale, Chapter 4 and 5) in the Western Indian Ocean. Case studies test specific ecological hypotheses using spatial pattern metrics quantifying seascape composition, configuration and terrain structure, which function as predictors for the occurrence and distribution of benthic assemblages and demersal fish.

Chapter 2 combines habitat mapping and spatial pattern metrics from seascape ecology to quantitatively test for and compare differences in seascape composition and configuration between five seamounts on the Southwest Indian Ridge (SWIR). Results quantitatively demonstrate that seamounts are highly variable in morphology, even when part of the same geological feature. As heterogeneity in the relative proportion and spatial relationships of habitats may influence ecological functioning, habitat mappers and marine managers focusing on representational protection of seamounts could benefit from such spatially-explicit approaches to quantify seabed heterogeneity.

Chapter 3 examines the influence of multi-scale seabed spatial heterogeneity on 15 commercially important fish families at three SWIR seamounts, focusing on patch affinity, patch complexity, patch size and seascape aggregation. Although strongly driven by site and depth, demersal fish respond to unique combinations of seascape composition, configuration and terrain structure depending on their family. Further, seascape composition and configuration (i.e. habitat size, shape and structural connectivity) had higher predictive power than terrain derivatives commonly used in developing proxies for deepwater fish biodiversity. These outcomes indicate the importance of incorporating spatial pattern metrics when identifying environmental predictors of fish distributions and suitable habitat in deep-sea environments.

Chapter 4 tests whether multi-scale geomorphology can act as a reliable spatial proxy for deeper reef assemblage (30 m-250 m) distribution. It found that assemblage occurrence and distribution is determined by a combination of environmental parameters, explained by the functional characteristics of each assemblage. Depth and structural complexity were main predictors, and broad scale predictors (25 m) proved more informative than finer scale predictors (2 m). Findings addressed geographical gaps in our knowledge of the distribution of deeper reef habitats and generated insights into ecological relationships. Complex geomorphological structures, including terraces and paleoshorelines, supported particularly high densities of mesophotic benthic assemblages and could be considered priority habitats for management.

Chapter 5 investigates the effect of fine-scale (cm-m) environmental heterogeneity on fish associated with mesophotic reefs (30 m-120 m). Spatial pattern metrics quantifying benthic composition, configuration and terrain structure were extracted from transect terrain models and orthomosaics produced with Structure-from-Motion (SfM) photogrammetry. In addition to known drivers (depth and geographic location), results show a combination of fine-scale seascape metrics of terrain structure, patch composition and patch configuration best explains mesophotic fish assemblage structure. Overall, sites with steep slopes and high terrain complexity hosted highest fish abundance and biomass.

Across case studies, spatial pattern metrics allowed quantification and comparison of seascape structure and functioned as reliable predictors for the occurrence and distribution of benthic assemblages and demersal fish at deeper reefs and seamounts in the Western Indian Ocean. Overall, spatial pattern metrics facilitated a better understanding of biodiversity-environment relationships in heterogeneous environments, in some cases functioning as the main explanatory variable. This thesis therefore recommends their further application in deep sea ecology, monitoring and ecosystem-based management and conservation, whilst accounting for the biological phenomenon under consideration and scale- and context dependency in survey and analysis.

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I would not be here were it not for the support of my personal network. I feel privileged to have come from a family that has instilled me with an awareness of the beauty of science and the natural world from an early age. Ultimately, these experiences and your support formed the foundations for embarking on this PhD journey in the first place. A special thanks to Mike, entering my life with unwavering support in ways large and small during the majority of my PhD.

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List of Abbreviations

2D, 3D . . . . . Two- or three-dimensional

ABMT . . . . . Area-based Management Tool

ABNJ, BBNJ . . Areas Beyond National Jurisdiction, Biodiversity Beyond National Jurisdiction

ALD . . . . . Aldabra, atoll and survey site in Seychelles

AUC-ROC . . . . Area Under the Curve of the Receiver Operating Characteristic, analytical technique to assess model performance

AUV . . . . . Autonomous Underwater Vehicle

BPA . . . . . Benthic Protection Area

BRT . . . . . Boosted Regression Trees, analytical technique

CBD . . . . . Convention on Biological Diversity

CWC . . . . . Cold-water coral

DBM, DTM . . . Digital Bathymetric Model, Digital Topographic Model

dbRDA . . . . . Distance-based Redundancy Analysis, analytical technique

DES . . . . . Desroches, atoll and survey site in Seychelles

(S)DM . . . . . (Species) Distribution Model

EBSA . . . . . Ecologically or Biologically Significant Marine Areas

ESP . . . . . Estimation of Scale Parameter, used in conjunction with ROC-LV

HOV . . . . . Human Occupied Vehicle, e.g. submersible, used for video surveys

IBM . . . . . Individual-based model

LiDAR . . . . . Light Detection and Ranging

LSI . . . . . Landscape Shape Index

MAE . . . . . Mean Absolute Error

MBES . . . . . Multibeam Echosounder

MCE . . . . . Mesophotic Coral Ecosystem

MPA . . . . . Marine Protected Area

MRF . . . . . Multivariate Random Forest, analytical technique

MRT . . . . . Multivariate Regression Tree, analytical technique

nMDS . . . . . non-metric multidimensional scaling, analytical technique

OOB . . . . . Out-of-Bag, used in relation to Random Forest validation

PCA . . . . . Principal Component Analysis

PDP . . . . . Partial Dependence Plot

PERMANOVA . Permutational multivariate analysis of variance

POI . . . . . Poivre, atoll and survey site in Seychelles

RF . . . . . Random Forests, analytical technique

(R)MSE . . . . . (Root of the) Mean Squared Error, used in relation to model validation

ROC-LV . . . . . Rate of Change in Local Variance, analytical technique

ROV . . . . . Remotely Operated Vehicle, used for video surveys

R-squared . . . . Proportion of variance in dependent variable explained

SDB . . . . . Satellite-derived bathymetry

SfM . . . . . Structure-from-Motion, in relation to photogrammetry

SIODFA . . . . . Southern Indian Ocean Deepwater Fisheries Association

StJ . . . . . St Joseph, atoll and survey site in Seychelles

SWIR . . . . . Southwest Indian Ridge

SWR . . . . . Shallow-water reefs (<30m)

TPI, BPI . . . . . Topographic Position Index, Bathymetric Position Index

TRI . . . . . Terrain Ruggedness Index

USBL . . . . . Ultra-short baseline

VME . . . . . Vulnerable Marine Ecosystems

VRM . . . . . Vector Ruggedness Measure

WIO . . . . . Western Indian Ocean.

1 Introduction

1.1 Rationale and aim

The ocean beyond the depth limits of most non-technical scientific diving and beyond the reach of most air- and space-borne optical sensors (i.e. $>$ 30 m depth) is the largest habitat on Earth, representing 66% of the planet's surface area. It provides various ecosystem services crucial to planetary health and societal well-being, including carbon sequestration and storage, nutrient cycling and the provision of food and energy resources (Thurber et al., 2014). As a result of the cost and logistical challenges of surveying the seabed, progress in ecosystem science at depths $>$ 30 m, considered "deep" environments in this thesis, has advanced less rapidly than in the ocean's more accessible shallow-water coastal regions. However, technological advances in seafloor mapping, ocean observing systems and deep sea exploration enable a growing scientific interest in deep seabed ecology and ecosystem-based protection of deep-sea biodiversity (Howell et al., 2020). Human activities are now a major driver of deeper marine ecosystem change (Halpern et al., 2019), with impacts having reached even the deepest parts of the ocean and capable of modifying seabed structure and associated biodiversity (Puig et al., 2012). A greater understanding of the structure and linkages between the seabed's spatial characteristics, biodiversity patterns, ecological functions, and the consequences of change is needed to inform ecosystem-based conservation and management plans (Danovaro et al., 2020).

Environmental heterogeneity, understood and measured as spatial or temporal variability in environmental conditions, is one of the main drivers of biodiversity and ecosystem functioning at the deep seabed (Zeppilli et al., 2016). Local and regional variability in environmental conditions has also been widely used as a proxy for the spatial distribution of seabed habitats and biodiversity, based on surrogacy: the fact that biophysical variable ranges (e.g. substratum type, geomorphology, temperature, light penetration) have a 'quantifiable correspondence' to benthic biodiversity (Harris,

2012b). The idea of surrogacy is grounded in niche theory (Hutchinson, 1957) which predicts that the occurrence of species and communities can be matched to specific combinations of environmental variables.

Quantification of environmental heterogeneity, its relationship to biodiversity patterns and their potential ecological effects is of key importance for ecosystem-based management of the ocean (Baker & Harris, 2012). Although seabed and habitat mapping researchers recognise the importance of the spatial structure of seabed habitat, few studies explicitly quantify spatial heterogeneity in environmental conditions to investigate its ecological consequences (Ismail et al., 2018). In addition to the financial and logistical challenges of sampling the seabed, our knowledge of seabed spatial patterns and processes has therefore also remained constrained by the conceptual models used to design surveys, formulate research questions and analyse data.

Whilst the biophysical environments of seabed and terrestrial landscapes differ, there is significant potential to combine existing seabed and habitat mapping research with tools and concepts from other terrain-oriented disciplines as landscape ecology and geomorphology to study the character and ecological consequences of environmental heterogeneity (Lecours et al., 2016b; Zajac, 2008). Seascape ecology evolved from landscape ecology and has led to new insights into structure-function relationships and spatially dynamic processes relevant to sustainable management (Pittman et al., 2021). However, unfamiliarity and scepticism of landscape ecology (Bell & Furman, 2017; Manderson, 2016), social and institutional barriers to cross-disciplinary communication and thinking (Paine, 2005)and limited data availability have resulted in relatively slow uptake in marine ecology compared to terrestrial ecology (Pittman et al., 2021). Studies that explicitly draw on the paradigmatic framework of seascape ecology have primarily focused on shallow coastal water areas (Boström et al., 2011; Wedding et al., 2011) (Fig. 1.1). Yet, some ecologists working beyond 30 m depth have started to make progress employing a seascape ecology framework to explore the ecological relevance of spatiotemporal patterns in seascape structure (Anderson et al., 2009; Goode et al., 2021; Price et al., 2021; Proudfoot et al., 2020; Robert et al., 2014; Teixidó et al., 2002; Zajac, 2008). Other authors have used landscape ecology concepts to provide new

insights on habitat heterogeneity and ecosystem functioning without explicitly citing landscape ecology or seascape ecology as a paradigmatic framework (Cordes et al., 2010; De Leo et al., 2014; Durden et al., 2015; McClain et al., 2011; Zeppilli et al., 2016).

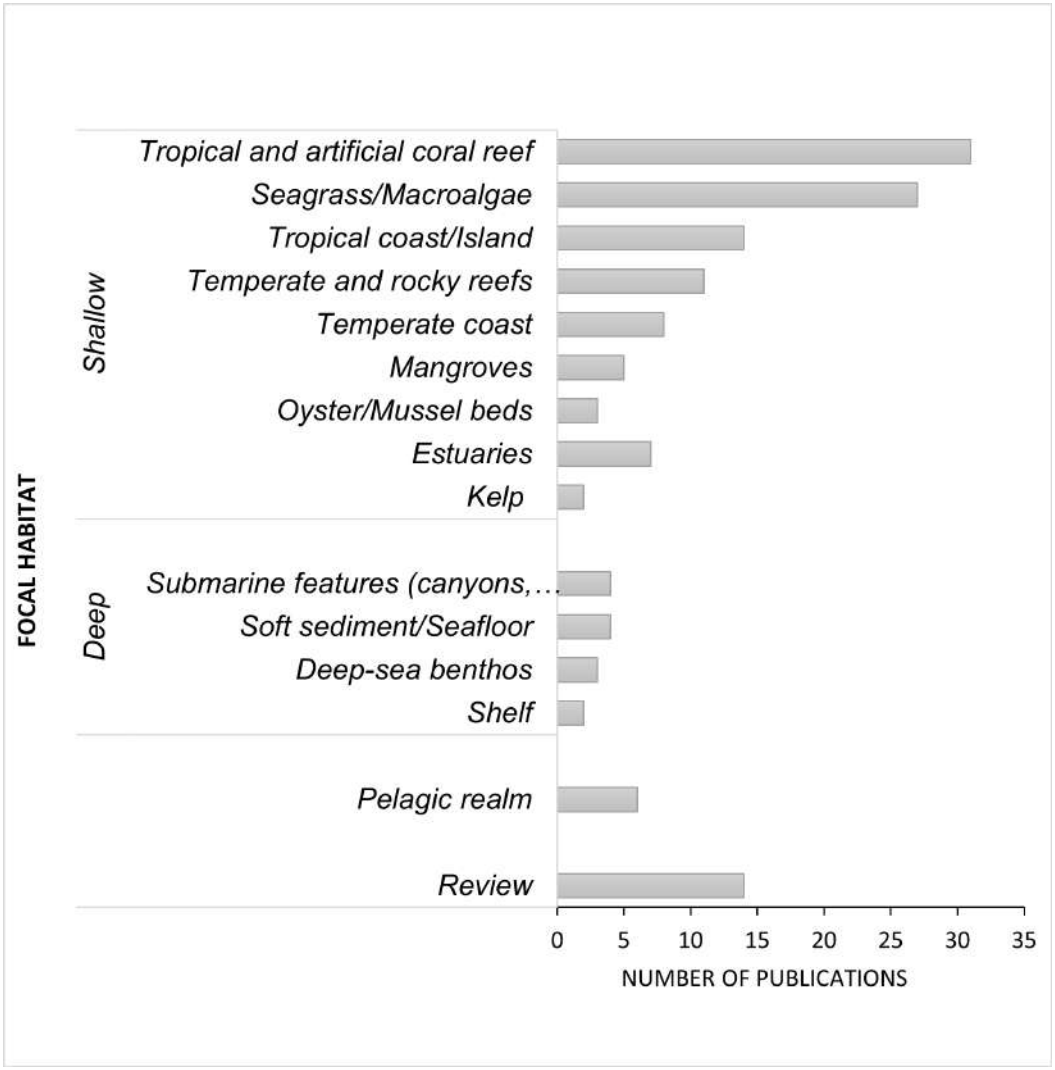


Figure 1.1: Google Scholar search (1990-2022) showing peer-reviewed studies that explicitly adopt the terms "seascape ecology", "marine landscape ecology" or "landscape ecology" in combination with "benthic", "seabed" or "seafloor" and classified by focal habitat type. 'Deep' studies were those beyond 30 m depth (relying on acoustic remote sensing), whereas 'shallow' studies were those above 30 m depth (accessible with optical remote sensing). These terms were selected to shed light on the on the number of studies that explicitly cite the field as an indicator of familiarity with the field. When shallow water studies incorporated multiple patch types (e.g. seagrass, coral and mangroves) these were classed under 'tropical coast/island'

This thesis explores how a seascape ecology perspective can improve our understanding of the character and ecological consequences of multiscale environmental heterogeneity in benthic seascapes beyond the depth limits of most non-technical

scientific diving and beyond the reach of most air- and space-borne optical sensors (i.e. > 30 m depth). To this end, this thesis first develops a conceptual framework to explore the ecological implications of multiscale environmental heterogeneity. It combines principles and methods from habitat mapping and seascape ecology (section 1.2), and identifies priority areas to facilitate the transition of seascape ecology to the deep seabed. These priority areas are the basis of objectives addressed in the remainder of the thesis, and are explored using case studies on seabed terrains characterised by high environmental heterogeneity: seamounts and atoll slopes (section 1.4). These complex submarine terrains often support increased biodiversity compared to the surrounding seabed, but knowledge gaps remain on the effects of spatial environmental heterogeneity in shaping their biodiversity. By combining seascape ecology, habitat mapping and spatial data analysis to map seabed terrain and habitats, quantify their spatial structure and relate heterogeneity to benthic and demersal biodiversity, this thesis will provide new insights in the transferability of seascape ecology to the deep seabed, simultaneously contributing to an improved understanding of spatial heterogeneity in seamounts and atoll slopes.

1.2 State-of-the-art: seascape ecology at the seabed

This section discusses the conceptual background, current status, potential and priority areas for seascape ecology at the deep seabed. First, the history of seascape ecology and sources of environmental heterogeneity at the deep seabed are explored. Although these patterns are interconnected with more dynamic pelagic processes in the water column through benthic-pelagic coupling (O'Leary & Roberts, 2018), this topic is mostly outside of the scope of this thesis. The remote sensing techniques most suitable for mapping the seabed and the different conceptual approaches (patch-based and gradient models) to model and quantify the structural patterns of seabed habitats are discussed. Then, the conceptual frameworks through which seascape ecology can provide insight into the ecological consequences of seabed and habitat heterogeneity are discussed, as well as the the potential for seascape ecology to inform ecosystem-based management. This includes a quantitative focus on the key concepts of seascape ecology:

composition and configuration, connectivity (horizontal and vertical), context, and consideration of scale (Pittman et al., 2021). Finally, priority research areas to advance the study of deep seabed environments using a seascape perspective are presented, and it is these that form the basis for the objectives of this thesis.

1.2.1 From landscapes to seascapes in ecology

Landscape ecology focuses on the causes and quantification of environmental heterogeneity – understood as temporal and spatial variation in environmental conditions - and its ecological consequences, considering landscape structure, connectivity, context, and scale (Turner, 2005). Importantly, landscape ecology, and therefore also seascape ecology, typically considers multiple scales of interest, often including analyses of spatial patterns at broader scales than other approaches in benthic ecology. In landscape/seascape ecology, a landscape or seascape is generally understood as 'an area heterogeneous in at least one factor of interest', most frequently represented and quantified as a mosaic of discrete internally homogeneous patch types (e.g. habitat patches, biotopes, patch mosaics) or a continuous surface (e.g. terrain structure, environmental gradients) (Turner and Gardner, 2015). Landscapes are defined not by geographic extent (i.e. there is no such thing as a fixed landscape scale or a landscape level) but rather by the scales(s) that are most relevant to the ecological phenomenon under consideration (Wiens, 1989). Over the past 50 years, landscape ecology has become well-integrated in mainstream terrestrial ecology, influencing how scientists and practitioners perceive and make decisions about terrestrial landscapes, including protected area design for biodiversity conservation (Turner, 2005; Wiens, 2009) and potentially serving as a sustainability science through informing human actions to address challenges of sustainability (Opdam et al., 2018; Pittman et al., 2021).

Although landscape ecology has traditionally focused on terrestrial and shallow aquatic systems, its research questions, methodologies and applications are also relevant to marine systems (Bell & Furman, 2017; Hinchey et al., 2008; Wedding et al., 2011). First proposed three decades ago as a way forward in understanding coastal biodiversity patterns (Ray, 1991), seascape ecology gradually developed as the marine counterpart

of landscape ecology to understand the causes, character and consequences of multiscale spatial and temporal heterogeneity in marine environments (Pittman et al., 2021). Despite significant biophysical differences between land and sea (Steele, 1989), concepts developed on land have proven relevant to marine systems, especially in the study of benthic pattern-process linkages and vice-versa (Barry & Dayton, 1991; Bell & Furman, 2017; Jelinski, 2015). Like terrestrial landscapes, benthic seascapes, sometimes referred to as marine landscapes or benthoscapes (Proudfoot et al., 2020; Zajac, 2008), can exhibit discrete patchiness and gradients in substratum characteristics and hence in the availability and quality of habitats (Bell & Furman, 2017; Harris, 2012a). In fact, foundational research in landscape ecology around landscape dynamics and disturbance emerged from studies of intertidal ecosystems (Levin & Paine, 1974). Seascape ecology, as practised by benthic ecologists, integrates analytical techniques from landscape ecology, including geomorphology, spatial pattern metrics, multiscale analyses, remote sensing, and habitat mapping to study the ecological relationships between seabed spatial environmental patterns and ecological processes (Pittman et al., 2021; Turner & Gardner, 2015; Wedding et al., 2011). Pelagic seascape ecology also draws on biological and physical oceanography (Kavanaugh et al., 2016).

Heterogeneity in seabed environments

Like shallow water environments, the deep seabed exhibits complex environmental heterogeneity in space and time that can be measured in the geology, sediments, topography, hydrodynamic and biogeochemical processes and other biological activity and disturbances (Table 1.1). Seabed topography influences exposure to the hydrodynamic regime, modifies sedimentation rates and shapes substratum characteristics and resulting settlement opportunities across spatial scales (Danovaro et al., 2014). Such heterogeneity influences habitat suitability for species and drives biological distributions, assemblage composition and the local and regional ecology across multiple scales and topographic structures as seeps, canyons, and seamounts may provide priority habitat (Borland et al., 2021; Levin et al., 2010). Dynamic processes in the water column such as currents and boundary layers, internal waves, thermal stratification, and gradients

and patchiness in various chemical and biological parameters (Cordes et al., 2010; Kavanaugh et al., 2016) influence seabed habitat through benthic-pelagic coupling (O'Leary & Roberts, 2018). The spatial patterning of benthic organisms also creates ecologically relevant biogenic structure on the seabed. For instance, cold-water corals shape distinct patches of structurally complex habitats, embedded in less vertically complex silt and sand sediments on which other animals depend (Price et al., 2021). Structural, chemical and physical disturbance effects, including direct human activities such as trawling and mining, further modify benthic seascape structure (Table 1.1). For example, fisheries trawling activity can physically damage or fragment biogenic patches formed by cold-water coral, altering habitat quality and availability sometimes with very low recovery rates (Huvenne et al., 2016; Puig et al., 2012). Seabed heterogeneity also influences the spatial patterning and rates of sedimentary biological processes that influence carbon sequestration and storage at the seabed, with implications for climate regulation (Snelgrove et al., 2018).

A seascape ecology framework for benthic seascapes

This review discusses the key conceptual and methodological attributes of a seascape ecology framework to study deep benthic seascape heterogeneity and its ecological consequences (Fig. 1.2). The first step is to develop research questions, which will drive data collection methodology and the evaluation of existing data types, including data quality, and careful consideration of spatial and temporal resolution(s) and extent(s). Important information sources are remote sensing data and statistical models (See 1.2.2: *'Sensing the seabed'* and 1.2.3: *'Mapping seabed habitats for ecological studies'*), to produce spatial models of seabed structure representing environmental and ecological heterogeneity. These are typically in the form of a patch mosaic or spatial gradients of environmental conditions (e.g. classified habitat maps, terrains) or a combination of both, depending on the question and phenomenon under consideration. Environmental structure in these maps and models can be quantified using spatial pattern metrics appropriate for the question and the relevant spatial construct (1.2.4: *'Representing*

Table 1.1: Examples of drivers of environmental heterogeneity in benthic seascapes

	Driver	Influence	Example
Geography	Latitude Longitude Shallow to deep gradients	Regional geological history and environmental gradients	Latitudinal, longitudinal and shallow-deep gradients of marine species richness (Gray, 2001)
Geomorphology	Topography/ Landform	Local environmental factors, flows, disturbances, geomorphic processes	Effect of different seabed morphologies on benthic biodiversity (Simon-Lledó et al., 2019; Zeppilli et al., 2016), the effect of sedimentary environment on community structure (Zajac et al., 2013)
	Geomorphic processes	Transport of organic and inorganic material - erosion, sedimentation	
	Sediment type and structure	Settlement opportunities, burrowing	
Oceanography	Hydrodynamics/ currents	Transport of nutrients and larvae, settlement opportunities	Ecological connectivity (O'Leary & Roberts, 2018), octocoral habitat suitability (Yesson et al., 2012), chemical gradients around seep environments (Cordes et al., 2010)
	Water chemistry	Nutrient availability, acidification, salinity	
	Temperature	Taxa specific thermal tolerances	
Ecology	Competition, predation, mutualism	Influences possible habitat space, food availability and biologically mediated ecosystem functions	Spatial structuring of benthic communities (Price et al., 2021; Teixidó et al., 2002), biologically mediated nutrient cycling (Snelgrove et al., 2018)
Disturbance	Dredging, trawling, mining, tectonic & sedimentary disturbance	Structural habitat alteration	Physical and biological impact of trawls on the seabed (Puig et al., 2012), effects of sedimentological processes on benthic ecosystems (Fontanier et al., 2018)
	Climate change	Ocean acidification, warming temperature, hypoxia, nutrient loading	Anthropogenic and climate change effects on the deep sea (Ramirez-Llodra et al., 2011)

and quantifying seascape patterns'). Through statistical analyses, pattern-pattern relationships and pattern-process relationships can be explored and tested based on core seascape ecology concepts of composition and configuration, connectivity, and context at a range of spatial and temporal scales (1.2.5: *'From spatial patterns to ecological processes'*). Finally, the results are interpreted, evaluated and applied to the research question.

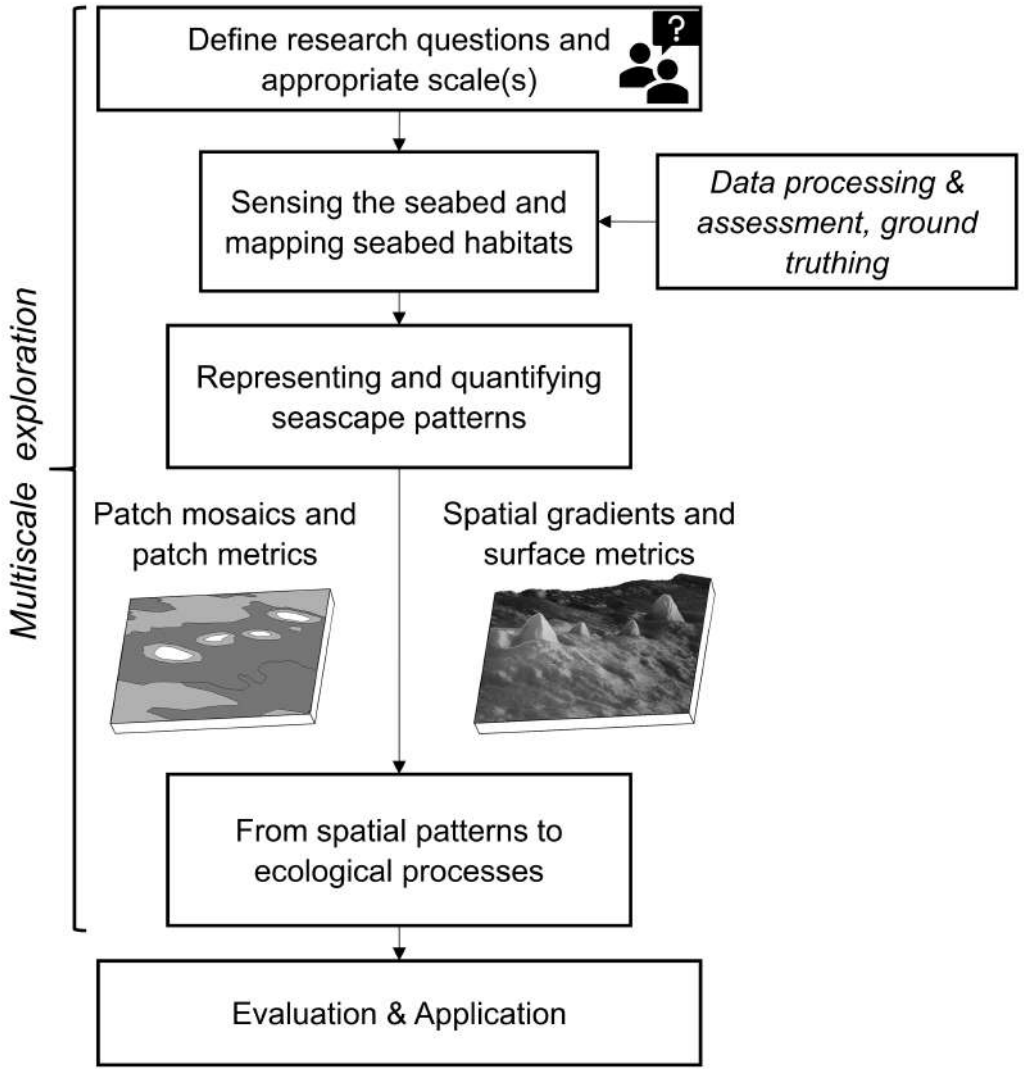


Figure 1.2: Example of the logical sequence of steps in a seascape ecology approach to study benthic seascapes in the deep sea.

1.2.2 Sensing the seabed

Geospatial mapping technologies

The geographical coverage provided by seabed maps, especially those representing geological characteristics, is rapidly increasing (GEBCO Compilation Group, 2021). Geospatial mapping technologies provide the primary data to generate seascape maps from which seascape patterns can be analysed. Therefore, selecting appropriate mapping tools and survey strategy is key in seascape ecology and should be guided by the question under consideration and desired outputs, the scale of analysis, and available technologies. A variety of remote sensing platforms and equipment is available to actively or passively survey seabed structure and is increasing the production of reliable seabed maps in the form of digital bathymetric models and georeferenced images (Fig. 1.3).

The majority of global ocean bathymetry datasets are constructed from satellite-derived gravity data (radar altimeter measurements), providing a relatively coarse scale (km^2) approximation of seabed terrain structure. Rather than resolving ocean depth directly, radar altimeters measure the distance between an orbiting satellite and the mean sea surface, which is influenced by gravity anomalies associated with topographic features of the seabed (Wölfl et al., 2019). In the coastal zone, satellite-derived bathymetry (SDB) is becoming a cost-effective technique to obtain high-resolution bathymetry to depths of up to 70 m in clear water by establishing a mathematical relationship between the surface reflectance of shallow waters in specific bands of the visible and infrared spectrum and depth. Satellite-derived bathymetry modelled with geographically weighted regression has been used to identify ecologically important seascape features across shelf ecosystems (da Silveira et al., 2020). Satellite (ICESat-2) and airborne laser altimetry (Light Detection and Ranging [LiDAR]) is also revolutionising shallow water bathymetric mapping, but these techniques are typically limited to 30-50 metres depth in optically clear water (Lepczyk et al., 2021).

Acoustic mapping technologies such as multibeam echosounders (MBES) used in this thesis are the main methods to acquire bathymetric data representing the spatial distribution of seabed depth. These acoustic mapping techniques can acquire considerably higher spatial resolution bathymetry (m) than satellite altimetry (25km) and passive

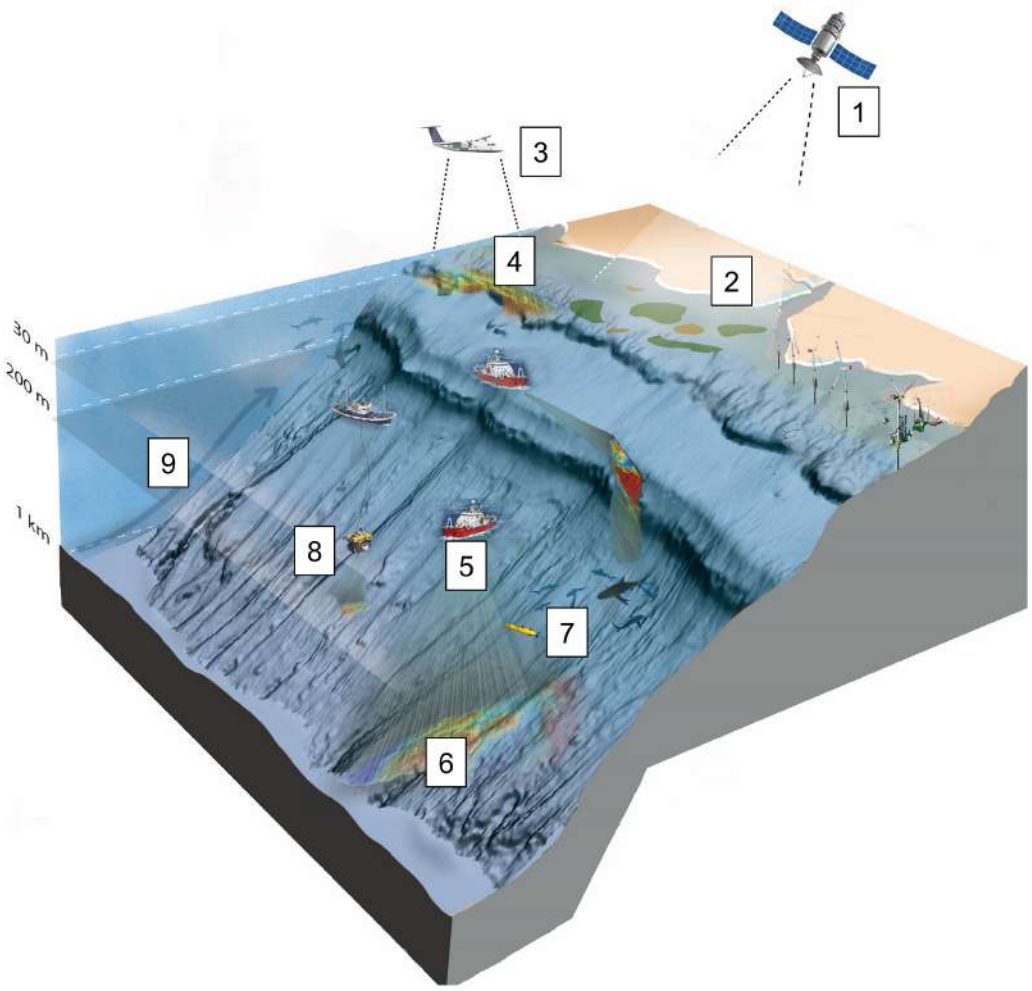


Figure 1.3: Examples of sensors to map seabed structure. Satellite data (1) can be applied to map patch-based structure (2) of shallow water environments (down to 30-50 m depth) and to create satellite-derived bathymetry. Air- and space-borne LiDAR (3) can produce accurate bathymetric data (4) of coastal shelf environments (30-50 m depth). Ship-mounted SoNAR (5) provides information on the continuous 3D structure of deeper seabed environments and slope environments at varying resolution and greater depths (6). At the finest scales, underwater AUVs (7) and ROVs (8) may be applied to map seabed structure (cm^2-m^2 resolution) using sonar and optical approaches such as subsea LiDAR and photogrammetry. Some water column patterns and processes relevant to seabed ecology can also be mapped, such as currents, internal waves and stratification (9).

optical sensors (limited to shallow waters). Sonar has proven particularly useful for seascape ecology studies linking bathymetric complexity to other surficial characteristics (e.g. substratum type from acoustic backscatter) and biological distributions in deep waters (Lecours et al., 2016a; Wilson et al., 2007). Acoustic and optical sensors may also be mounted on autonomous underwater vehicles (AUVs), remotely operated vehicles

(ROVs) or human-occupied vehicles (HOVs) for high-resolution mapping of seabed and water column structure including biota (Fig. 1.3). For mapping purposes, underwater vehicles are most commonly equipped with MBES (Robert et al., 2017), but subsea LiDAR systems rated to depths of over 3000 m are now also becoming available (Filisetti et al., 2018). Fine-scale photomosaics, stereo-photography and Structure-from-Motion (SfM) photogrammetry map the seabed at sub-metre scale using cameras mounted on underwater vehicles and are demonstrated later in this thesis. These cost-effective image processing techniques are particularly useful for investigating fine-scale (millimetres to metres) linkages between terrain structure and biodiversity, even on vertical seafloor terrain (i.e. steep banks and canyon walls) (Price et al., 2021, 2019; Robert et al., 2017).

Biological data collection and image processing

Although geospatial mapping tools can provide broad-scale and continuous information on bathymetry and other indirect measurements of seabed structure, used in isolation they often lack biologically detailed information about the seabed required for ecological studies. When available, detailed and georeferenced in situ observations on biological components (species and assemblages) and abiotic characteristics (substratum type, geology) are extremely valuable, even if geographically sparse. Conventional biological survey methods for studying the benthic environment, such as grab samples or photo/video observations typically provide point samples or transects covering a relatively small area of seabed, resulting in detailed but patchy data (Brown et al., 2011). Methods available to obtain ground-truthing on ocean ecology and environmental conditions, including grabs, cores and non-destructive underwater video observations, have been reviewed elsewhere (Danovaro et al., 2020; Woodall et al., 2018).

Here underwater vehicle-mounted georeferenced benthic video and photography are highlighted as these are a non-destructive technique to collect georeferenced deep seabed observations and the main technique used in this thesis. Camera systems can be deployed using stationary (e.g. drop cameras or landers) and mobile platforms (e.g. ROV or AUV), and mobile image data is typically collected in the form of a transect. For all platforms, a system to record geographic position (e.g. Ultra-Short Baseline

(USBL) or estimation from vessel GPS), is crucial to link observed biodiversity and environmental conditions. Spatial scaling can be obtained through laser scales, exact measures of the camera set-up, or through stereo image systems. The annotation process extracts physical, biological and ecological data of interest such as taxonomic presence and absence, diversity and biomass, animal behaviour, sediment type and habitat structure. When accurate identification is not possible, species observations are recorded as morphospecies or morphotype, and international efforts are emerging to develop common standards and reference guides to identify marine morphotypes (Howell et al., 2020). Advances in marine visual imaging have greatly increased the efficiency of data collection from marine surveys, and significant developments continue in computer vision and automated classification (Durden et al., 2021).

1.2.3 Mapping seabed habitats for ecological studies

A key challenge in seabed ecology is the scale discrepancy between the capability to measure 1) spatially continuous measures of the physical aspects of the seabed (i.e. bathymetric surveys); 2) comparatively fine-scale biological point samples and transect data (photos, videos, grabs, cores); 3) the scale(s) relevant to the ecological processes under investigation; and 4) the scale at which marine spatial management and conservation takes place. Benthic habitat mapping combines environmental datasets reflecting seabed topography (bathymetry) and substratum type (using the strength of acoustic backscatter as a proxy) and, when available, in situ ground-truthing of biology and seabed characteristics. Using multiscale terrain derivatives as spatial proxies, surrogates or indicators of species and habitat distributions, seabed habitat mappers aim to produce spatial representations of the potential occurrence and distribution of seabed habitats (Brown et al., 2011). A seabed habitat is an area defined by physical, chemical and biological parameters that may correspond to environmental preferences of a species or group of organisms at particular temporal and spatial scales (Lecours et al., 2015). Parameters in the overlying water column that structure seabed habitat distribution may also be sampled by sensors (e.g. Acoustic Doppler Current Profiler) or estimated through physical models (Pearman et al., 2020). Habitat

maps in their many forms are enabling tools in seascape ecology, as they visually represent spatial patterns and provide an opportunity to quantify seascape structure at multiple scales. There are three main habitat mapping approaches for deep seabed environment that display biological distributions as categorical classes or continuous probability distributions (Table 1.2).

Table 1.2: Habitat mapping approaches in seabed environments and selected applications

	Output	**Seascape Ecology Relevance**	**Example**
Top-down	Discrete classification into areas of similar environmental characteristics corresponding to potential habitats	Classification of seabed surface morphology and substrate proxies to allows for quantification of terrain composition and configuration (2D)	Submarine Canyon habitat characterisation (Ismail et al., 2015), MPA prioritisation (Hogg et al., 2016) and coastal habitat and substratum characterisation (Calvert et al., 2015; Shumchenia & King, 2010), occurrence of geomorphological seamount habitats (chapter 2)
Bottom-up	Discrete classification into potential habitat patches incorporating ground-truthing data	Classification of habitat types allowing for characterisation of composition and configuration (2D), characterisation of ecology-environment relationships	Distribution of benthic habitats on fishing ground (Buhl-Mortensen et al., 2009), sponge and coral habitats (Neves et al., 2014) and coastal habitats and substratum (Calvert et al., 2015; Shumchenia & King, 2010), occurrence of benthic substratum types (chapter 5)
Predictive	Continuous probability distribution of species or habitats	Characterisation of species-environment relationships (2D/3D) and resulting distribution patterns, filling geographical knowledge gaps	Distribution of cold-water corals (Robert et al., 2016; Ross & Howell, 2013), distribution of deeper reef communities (chapter 4)

Top-down and bottom-up habitat mapping

Top-down and bottom-up habitat maps both segment the seascape in categorical classes representing seabed habitats but differ with respect to the inclusion of ground-truthing data. Top-down habitat mapping (unsupervised approaches, marine landscape mapping or abiotic surrogate mapping) has developed as a response to limited availability of

biological data in offshore environments (Verfaillie et al., 2009). It relies on segmentation and classification methods to identify patterns in seabed attributes and discriminate between potential habitats, traditionally covering large areas lacking biological data. This approach assumes that the same factors that shape environmental patterning shape habitats (Shumchenia & King, 2010) and outputs show the distribution of spatially discrete areas classified as patch types and potential habitats. Environmental characteristics (lithology, relief, grain size, bedforms, geological history and bottom water characteristics) distinguish habitat types (McArthur et al., 2010). Top-down approaches are particularly useful for seascape studies where ground-truthing data is absent or discontinuous and have, for example, been used for the characterisation of seascape structure (Ismail et al., 2015) and the design and evaluation of potential MPAs (Hogg et al., 2016). When available, biological data may be used to classify and ground-truth the map post hoc and assess its ecological relevance by modelling biological characteristics against map units or classes (Hogg et al., 2018).

Bottom-up habitat mapping (supervised approaches) integrates ground-truthing data in the segmentation and classification process, rather than applying it post hoc. Biological ground-truthing data, for example, is first organised in classes corresponding to assemblages or community types using clustering (e.g. Shumchenia & King 2010), ordination (e.g. Buhl-Mortensen et al. 2009) or hierarchical habitat classification schemes (e.g. Calvert et al. 2015). Community-environment relationships are then used to segment continuous environmental variables in distinct map units representing potential habitat class occurrence and distribution. Ground-truthing data may also take the form of substratum classes to map the distribution of discrete substratum types. An appropriate definition of classes (thematic resolution) is essential as the classification type can influence map outcomes (Strong et al., 2019). Likewise, it is important to ensure that the ground truthing (analytical scale) is appropriate for the scale of the remotely sensed data (observational scale) to avoid possible scale mismatches. Machine learning algorithms (e.g. Random Forests, Boosted Regression Trees, Artificial Neural Networks, Support Vector Machines) have advanced the accurate

classification of benthic seascapes and can be very effective even in data-poor regions with limited ground-truthing data (Turner et al., 2018).

Spatial predictive mapping

Spatial predictive mapping or distribution modelling (DM) approaches produce continuous probability data on the occurrence and distribution of the species or habitat of interest (Elith & Leathwick, 2009). DMs are increasingly applied in the marine environment to model and predictively map individual species, habitats, and biological assemblage metrics such as abundance, biomass, diversity, and functional traits across geographical space. DMs help explain the multiple interacting drivers of biological distribution patterns and forecast environmental change consequences (Melo-Merino et al., 2020). At the deep seabed, DMs also offer great potential to address spatial data gaps, but face challenges associated with a limited availability of ground-truthing data and relevant and reliable spatial predictor data. The majority of DMs are correlative, building on species-environment relationships extracted from known occurrence locations and constructed using statistical approaches (e.g. Generalized Linear Models (GLMs), Generalized Additive Models (GAMS)), machine learning (e.g. Random Forests, Boosted Regression Trees), the MaxEnt package, or multi-model ensemble approaches (Robert et al., 2016). Varieties of these approaches have been applied effectively to seabed environments where much of the application of DM techniques has been to map distributions of cold-water corals (Kenchington et al., 2019a; Robert et al., 2016) (Table 1.2).

1.2.4 Representing and quantifying seascape patterns

Although deep seabed researchers have long recognised the importance of seabed habitat heterogeneity (e.g., the combination, abundance and spatial orientation of different geophysical, chemical, and biological habitat types), it is rarely quantified explicitly (Ismail et al., 2018). In seascape ecology, spatial pattern metrics are applied routinely to quantify spatial heterogeneity, monitor and compare seascapes, predict species and diversity distributions, and provide a starting point to relate seascape

patterns to ecological processes (Lacharité & Brown, 2019; Lausch et al., 2015; Pittman et al., 2021). Patch mosaic and continuous gradient representations are the most often used paradigms to quantify patterns from benthic habitat maps and terrain models, and are crucial enabling tools for the application of seascape ecology (Lepczyk et al., 2021; Wedding et al., 2011).

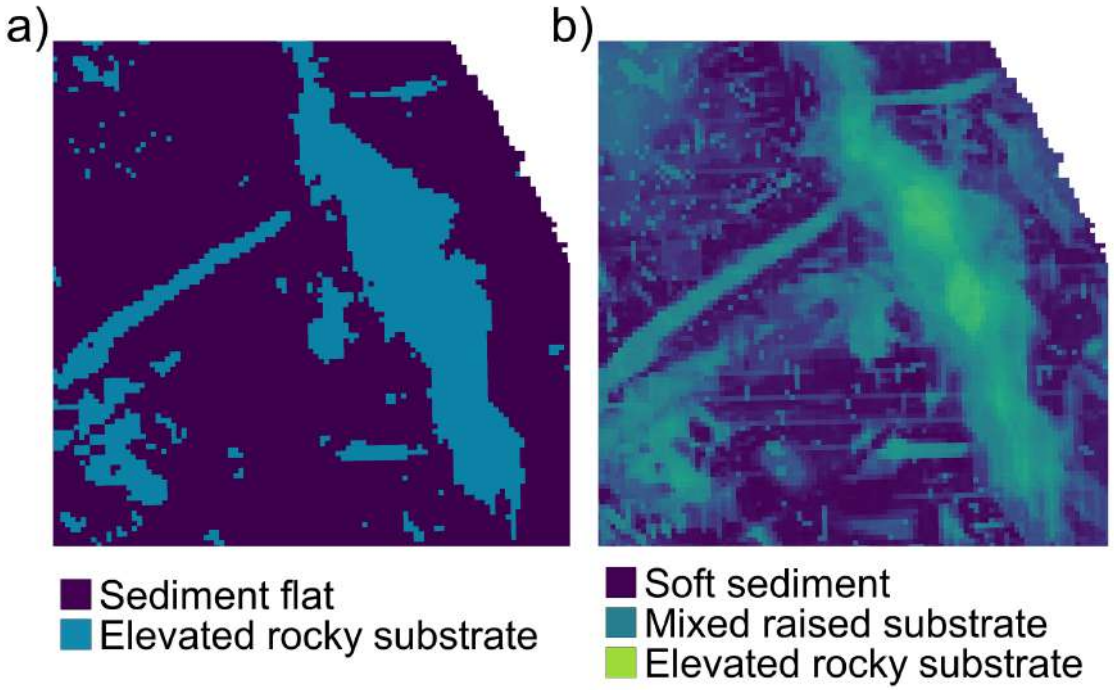


Figure 1.4: Patch-mosaic (a) and continuous gradient (b) representations of seascape structure produced using bathymetry collected around Aldabra atoll, Seychelles, between 150 m and 500 m depth. The patch mosaic representation homogenizes within-patch variability and enhances discrete edges, while the gradient model preserves the continuously varying heterogeneity across the seascape

Choice of spatial paradigm to represent seascapes

The choice of conceptual framework and associated spatial model(s) of seabed heterogeneity to address research questions is key to the methods and interpretation of results. Patch-based models, conceptually derived from terrestrial vegetation mapping, represent seascapes as a two-dimensional surface of discrete patches, each with internally homogeneous environmental conditions and typically with sharp patch boundaries (Fig. 1.4a) (Cushman & McGarigal, 2008; Forman, 1995). Patch-based models have been

applied widely in ecology and have been central to applications of the Theory of Island Biogeography (MacArthur & Wilson, 1967) and landscape ecology (Lausch et al., 2015). In benthic environments, categorical or thematic habitat maps are typically either patch-matrix or patch-mosaic models. The patch-matrix model represents focal habitat patches as embedded in an 'inhospitable matrix' that is likely to spatially constrain some ecological processes such as individual animal movements of habitat type specialists (e.g., obligate reef species). Patch-matrix theory has for example been used to discuss the theoretical importance of rocky patches in sedimentary abyssal environments (Riehl et al., 2020) and may serve to elucidate metapopulation dynamics, with appropriate habitat patches functioning as 'sources' and 'sinks' driving the dispersal, assembly and diversity of species and populations (Puckett & Eggleston, 2016). The patch-mosaic model emphasises that the composition (amount and variety of patch types) and spatial configuration (spatial arrangement of patches) of the seascape unit as a whole influences ecological functioning (Wiens et al., 1993). The patch-mosaic model is an important paradigm for explaining local biodiversity in deep-sea benthos, with patches of environmental characteristics such as substratum, disturbance and nutrient availability jointly controlling biodiversity (Grassle, 1989). However, many benthic systems, most notably soft-sediment terrains, also exhibit spatial gradients and ecotones in seabed characteristics and environmental conditions (Brown et al., 2011; Kågesten et al., 2019; Zajac, 2008). Fuzzy classification recognises that benthic habitats are separated by transition zones or transient boundaries rather than sharp edges (Lecours et al., 2015; Lucieer & Lucieer, 2009). Although intuitive, the patch-mosaic model may hinder the ability to detect species' responses to such gradients of heterogeneity (McGarigal & Cushman, 2005).

In contrast, the spatial gradient or continuous surface model has been advanced in landscape ecology as an alternative to patch-based models (Fig. 1.4b) and represents seascapes as continuously varying surfaces without discrete patch boundaries (Wedding et al., 2011). The gradient model avoids the homogenisation of potentially important within-patch complexity and the problem of ecologically arbitrary classification that can occur in categorical habitat classifications (McGarigal & Cushman, 2005; McGarigal

et al., 2009). The gradient model recognises that many organisms and ecological processes respond to a gradual multiscale variation in spatial heterogeneity, consistent with niche-based gradient theory (McGarigal & Cushman, 2005). For example, a study in seep environments demonstrated macrofaunal abundance and diversity responded to gradients of chemical conditions (methane fluid flow) in addition to biogenic patch character (Cordes et al., 2010). With 2.5D digital bathymetric models being the primary data layer to study seabed structure, continuous gradient models are already routinely applied in seabed environments to produce habitat maps and distribution models by applying surface metrics from marine geomorphometry (Lecours et al., 2016b). Increased application of fine-scale survey techniques such as laser scanning and photogrammetry to seabed environment also enables the construction of true volumetric 3D reconstructions of continuous seascape structure (Lepczyk et al., 2021). 3D representations may capture additional ecologically relevant aspects of seascape structure, and have been used in the deep sea to quantify surface area covered by cold-water coral (Fabri et al., 2019), and in chapter 5 to quantify structural patterns of mesophotic coral ecosystems.

Whether to represent seascapes as continuous gradients of environmental and biological conditions or as patch-matrix or patch-mosaic depends on the research question's conceptual framework, data availability and quality and the ecological phenomenon under consideration (McGarigal et al., 2009; Wedding et al., 2011). Both patch-based and gradient model approaches have successfully been applied to understand biophysical drivers of habitats and species in the marine environment (Ferrari et al., 2018). Because both patch-mosaic and gradient models represent ecologically relevant patterns, an integrated patch-gradient model framework that includes individual metrics derived from both models can offer further insight into ecological consequences of environmental heterogeneity (Sekund & Pittman, 2017). Models predicting coral reef fish distributions in Hawaii that combined 2D and 3D explanatory variables outperformed models with only 2D or 3D variables (Wedding et al., 2019). Likewise, in deep water across Cordell Bank in California, demersal

fish responded to discrete patchiness and patch context across continuous gradients in seabed terrain character (Anderson et al., 2009).

Spatial pattern metrics for quantifying seabed heterogeneity

A wide range of metrics are available for quantifying the spatial structure of the seascape represented in either a patch-based or gradient model (Frazier & Kedron, 2017)(Table 1.3) and computing tools are available to aid multiscale analyses (McGarigal et al., 2012; Walbridge et al., 2018).

Patch-based metrics can be categorised broadly into composition (i.e. number of patch classes and their abundance in the seascape) and configuration (i.e. spatial arrangement, orientation, and shape of patches in the seascape). Additionally, they can be applied at different levels of structural organisation to quantify attributes for 1) individual patches, 2) patch classes (all patches of the same type) or 3) an entire seascape unit (i.e. measures of seascape composition and configuration) (Gustafson, 2019). Patch metrics enable researchers to quantitatively explore and describe the spatial structure of the benthic environment at a wide range of depths and spatial scales. For example, patch size and variability, patch diversity and patch interspersion emerged as key variables to characterise the fine-scale (1 m^2) spatial patterning of Antarctic benthic communities (Teixidó et al., 2002). At broader scales, spatial configuration metrics including contagion (clumping of attributes) functioned as a spatial proxy for biodiversity when comparing the spatial heterogeneity among branches of a submarine canyon (Ismail et al., 2018). Patch metrics also have specific applications in understanding the effect of seabed patterns on the distribution of species and the composition of species assemblages including structure, richness and diversity. In the Cape Howe Marine National Park (Victoria, Australia), seascape composition and configuration combined with depth explained 35% of variation in demersal fish assemblage, indicating that combinations of both patchy and contiguous habitats maximise fish diversity and abundance (Moore et al., 2011).

Table 1.3: Spatial pattern metrics applied to patch-mosaic and continuous gradient models, with selected examples

	Examples of metrics	Measures	Ecological importance	Selected examples
2D- composition	Patch size	The area of each patch	Information on basic area requirements, an indicator for species richness	• Composition of Antarctic benthic communities: (Teixidó et al. (2002)
	Patch richness	Number of patch types in the landscape	Information on the representation of different habitat types	• Quantification of seascape spatial heterogeneity Ismail et al. (2018), chapter 2
	Patch proportion or evenness	The proportional abundance of each patch in the landscape	Species richness, habitat fragmentation	• Comparison of spatial heterogeneity: chapter 2
	Shannon's or Simpson's Diversity Index	Landscape diversity – dependent on the number of patches and proportion	Proxy for species diversity, spatial configuration, resilience to disturbances	• Fish-habitat associations and distribution of demersal fish: Anderson et al. (2009); Moore et al. (2011), chapters 3 and 5
2D- configuration	Edge to area ratio	Length of edge segments	Proxy for edge effects	• Distribution and diversity of megabenthic invertebrate communities: (Robert et al. (2014, 2016); Zajac et al. (2013)
	Core area	The patch area away from a buffer zone	Habitat quality	• Evaluation of structural connectivity: Proudfoot et al. (2020)
	Shape index	The geometric complexity of the patch	Seascape complexity, edge effects	
	Contagion	A measure of landscape clumping	Dispersion of landscape, metapopulation dynamics	
	Interspersion and juxtaposition index	A measure of the intermixing of different patch types	Seascape connectivity, dispersal	
	Proximity index	A measure of patch isolation	Seascape connectivity, dispersal	
	Fragmentation index	A measure of landscape splitting	Disturbance to habitat structure	
2.5D- Terrain structure	Slope	Elevational change	Local hydrodynamic regime (exposure, food supply), the stability of surface	• Habitat mapping: Hogg et al. (2018, 2016); Ismail et al. (2018, 2015), chapter 2
	Mean depth	Distance to the ocean surface	Proxy for physical processes including temperature, light penetration, sedimentation	• Biodiversity-habitat associations: Borland et al. (2021); Durden et al. (2015); Simon-Lledó et al. (2019), chapter 3 and 5
	Aspect	Orientation of surface	Exposure to currents, sedimentation	• VME distribution: (Robert et al., 2016; Ross & Howell, 2013), chapter 4
	Seascape curvature (BPI)	Orientation and relative elevation of the surface	An index measuring exposure/shelter	• Fine-scale habitat complexity: (Price et al., 2019), chapter 5
	Habitat complexity (rugosity, VRM)	Critical for ecological functions and habitat prediction	Settlement opportunities, microhabitats, shelter from exposure	
3D	Surface Area	Total area that surface of object occupies	Descriptor of habitat structure	• Quantification of reef surface area (Fabri et al., 2019)
	Volume	Three-dimensional space that object occupies		

Despite their demonstrated ecological relevance, patch-based metrics have found limited application in explaining the functional relevance of heterogeneity observed across deep seabed environments compared to shallow water environments (Ismail et al., 2018; Robert et al., 2014). Marine geomorphometry methods and metrics are more widely applied to describe and analyse deep seabed spatial patterns from digital bathymetric models, and are readily accessible in common GIS software and open-source statistical computing code (Lecours et al., 2016b; Lucieer et al., 2018). Geomorphometrics (also referred to as terrain metrics or surface metrics), measuring slope, orientation, curvature and terrain complexity, have been identified as key drivers of seabed biodiversity patterns and ecological processes over multiple scales (Bouchet et al., 2015; Brown et al., 2011; Wilson et al., 2007). For example, terrain slope has been used as a key predictor of global habitat suitability and distribution for six orders of cold-water octocoral (Yesson et al., 2012) and to identify elevational gradients associated with high megafaunal biodiversity in abyssal environments (Durden et al., 2015). Working with continuous gradients offers analytical flexibility, including greater opportunity for creating derivative metrics (e.g. range, maximum, minimum, standard deviation), multiscale analyses and capturing emergent ecological properties of multiple metrics (McGarigal et al., 2009). DM outputs can be interpreted as continuous habitat suitability surfaces (McGarigal & Cushman, 2005), from which patterns can be quantified and incorporated in further ecological analyses. For example, a study around Hoburgs Bank in the Baltic Sea demonstrated that continuous probability maps of seabed substratum and biodiversity were valuable inputs for further benthic classification such as applying thresholds (Kågesten et al., 2019). Although predicted patterns from DMs are rarely explored with pattern metrics, additional analysis and examination of ecological implications is an interesting area for future research attention.

Regardless of the choice of conceptual model and associated metrics, key considerations for the selection of spatial pattern metrics should be their ecological relevance as driver or proxy (Kupfer, 2012) of the phenomenon under consideration (Lecours et al., 2016a), the sensitivity of the data to interpretation rules and interdependencies, and any redundancy of indices (Cushman et al., 2008; Turner, 2005). In metric

extraction, researchers should consider neighbourhood sizes and temporal, spatial and thematic resolution of mapped data, scale-dependent effects on pattern metrics that may influence the results of ecological analyses, as well as error propagation (Kendall et al., 2011; Moudrý et al., 2019). To facilitate comparative studies and robust interpretations of the seabed and associated biological communities, researchers should explicitly address their methodology in choosing terrain metrics and extracting them, the ecological rationale behind scales chosen and analysis techniques (Lecours et al., 2016a). Regardless of the metrics applied, the choice of statistical technique can influence spatial predictions. Robert et al. (2016) identified technique-specific predicted patterns in habitat suitability for cold-water coral species assemblages on the Rockall Bank (NE Atlantic) when comparing results from multiple techniques and with highest performance achieved with an ensemble of all model outputs.

As seabed habitat suitability and species distributions are strongly influenced by dynamic temporal and spatial heterogeneity in the overlying water masses, for example in the form of current exposure, water chemistry, nutrient concentration and tidal regimes (Yesson et al., 2012), seascape metrics of seabed characteristics alone are unlikely to explain all biological variation. Therefore, an important future focal area in seascape metric research is developing and integrating pelagic metrics measuring continuous structure and patchiness in the overlying water column, for example, from remotely sensed satellite data or physical models (Alvarez-Berastegui et al., 2016; Kavanaugh et al., 2014). For example, predictive models incorporating high-resolution hydrodynamic data (baroclinic and barotropic current speed, salinity, temperature) in Whittard Canyon, NE Atlantic, explained more variation in cold-water coral species richness, abundance and diversity compared to models constructed with topographic parameters alone (Pearman et al., 2020).

1.2.5 From spatial patterns to ecological processes

Like terrestrial landscape structure, seabed structure – the abundances, combination, spatial orientation and variation in geophysical and biological habitat - influences the spatial flows of matter, energy and organisms and other critical ecological processes that

shape ecosystem functioning (Barry & Dayton, 1991). Therefore, seascape heterogeneity facilitates, hinders or constrains key ecological processes such as species dispersal, establishment, resource acquisition, reproduction and metapopulation dynamics, and the horizontal and vertical connectivity between seabed ecosystems. This section introduces how seascape ecology can provide insights into the ecological consequences of seabed heterogeneity through the concepts of 1) seascape structure, comprising composition, configuration and terrain variability; 2) seascape connectivity; 3) seascape context; and 4) scale considerations (Figure 1.5).

Seascape structure: the ecological importance of patch mosaics and terrains

Seascape structure, the spatial composition and multi-dimensional configuration of the seascape, has been the focus of seascape ecology efforts to quantitatively link seascape heterogeneity to biological distribution patterns, organism movements and other ecological processes (Pittman et al., 2021; Wedding et al., 2011). From a seascape ecology perspective, seascape structure comprises three main concepts: 1) composition (the variety and relative abundance of patch types), 2) spatial configuration (the spatial arrangement of patches) and 3) terrain structure (variations in seabed depth) (Figure 1.5a), which all are measured using spatial pattern metrics applied to habitat maps and/or terrain models (Table 1.3).

In shallow-water systems, studies relating seascape structure to marine organisms through spatial pattern metrics have successfully generated new insights on species-specific responses to seabed heterogeneity (Boström et al., 2011), structure-mediated animal movement behaviour (Hitt et al., 2011), the effects of seasonality and life stage (Staveley et al., 2017), predator-prey dynamics (Hovel & Regan, 2018) and the genetic structure of marine species (Van Wynsberge et al., 2017). Understanding the implications of seascape structure for the distribution of species and habitats and ecological processes is equally of interest to ecologists working in deeper waters, with habitat heterogeneity a long recognised key research topic (Grassle, 1989; Levin et al., 2001). Important knowledge gaps remain about patch size, patch spacing and crucially, the drivers and implications of such spatial patchiness (Cordes et al., 2010; Kaiser

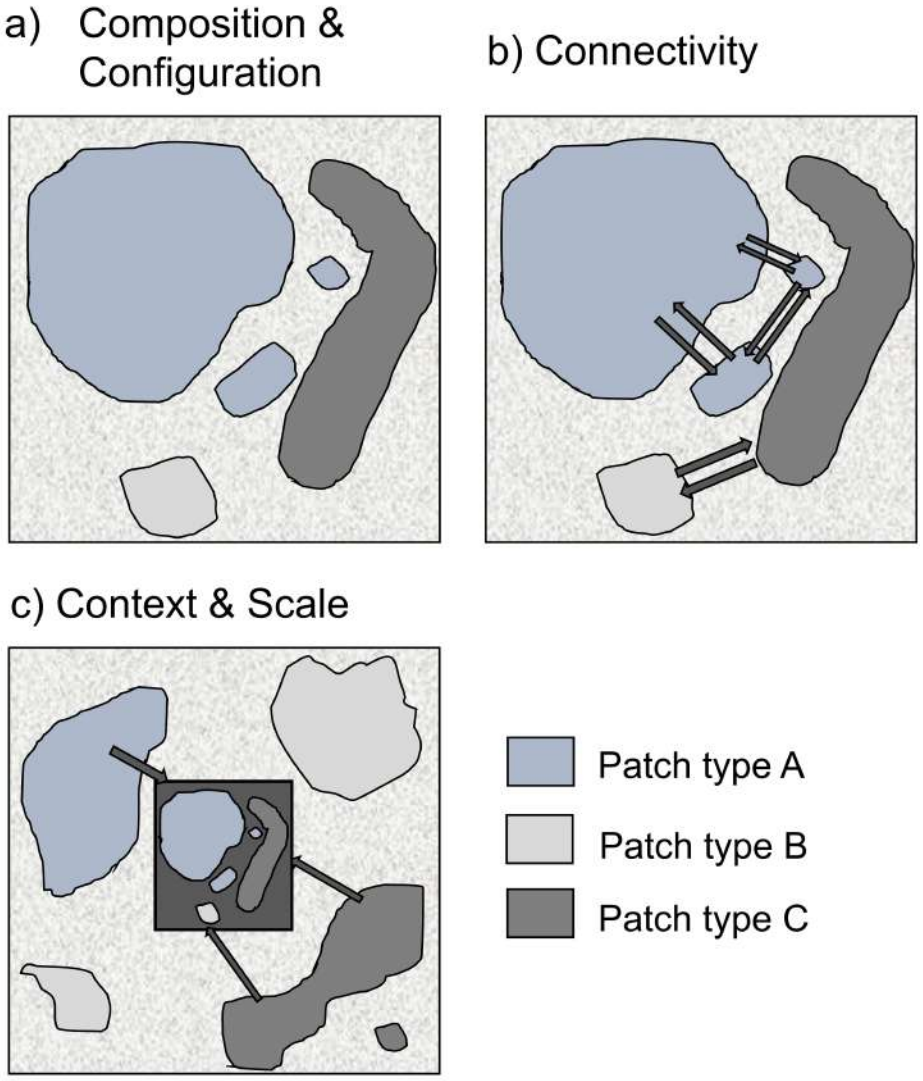


Figure 1.5: Schematic representation of patch-based seascape structure at the seabed, based on the patch-matrix model. Seascapes differ in the composition and configuration of habitats (a), such as their size and shape, which influences processes as connectivity in the seascape (b). The surrounding environment (c) has further effects on ecological flows within the seascape under consideration

& Barnes, 2008). Seascape ecology can contribute to addressing these knowledge gaps through assessing the potential effects of seascape composition, configuration and terrain structure (Harris, 2012a).

Seascape composition

Considering the effects of seascape composition, focusing on the size, abundance and diversity of patches represented in habitat maps, is key to understanding the

types, diversity, richness and abundance of assemblages that the seascape may support (Turner & Gardner, 2015). In terms of size, studies in terrestrial systems indicate that larger habitat patches can support more abundant and biodiverse assemblages because within-patch environmental variability increases with area (Harris, 2012a). Patch size effects have also been examined in deep sea environments. For example, underwater camera surveys examined the abundance of marine species living on glacially deposited rocks ("dropstones") of varying size, that form distinct habitat patches in a more homogeneous seascape (Ziegler et al., 2017). Relating patch size to assemblage characteristics, the study concludes that dropstones form local biodiversity hotspots with diversity and abundance of organisms predictably increasing with dropstone size following the Theory of Island Biogeography. It is well-understood that the diversity of habitat classes shapes biological assemblages. For example, abyssal patches of rocky substratum host different benthic communities than the surrounding sedimentary environment (Riehl et al., 2020). Accounting for the diversity of patch types (e.g. soft sediment, rock, boulders) and broad-scale zones (e.g. slope, bank or shelf) is important in determining the presence, diversity and abundance of mobile species that use more than one patch type during their life cycle (Anderson et al., 2009).

Seascape configuration

Seascape configuration, the shapes of habitats and their physical arrangement in the seascape, adds to seascape composition to influence ecological processes. It can provide insights into habitat suitability and patches' capacity to function as a connected network. Evidence from shallow coral reef ecosystems demonstrates that the configuration of patch types across seascapes influences species distributions and the structure of biological assemblages. For example, the proximity of mangrove habitat to seagrass habitat strongly influenced fish density by facilitating resource availability and organism movement (Berkström et al., 2013; Pittman et al., 2007). Configuration has also been linked to ecosystem services such as food provisioning and carbon storage, with highly connected seascapes storing larger amounts of organic carbon in sediment (Asplund et al., 2021).

Patch shape influences habitat suitability through the availability of core and edge habitat (transition zones between patch types). Because more complex habitat shapes feature a higher proportion of edges, they typically have increased exposure to external disturbances and edge effects. Edge effects, such as exposure to currents and turbidity, create ecotones at patch edges and reduce the availability of core habitat which might disadvantage species dependent on that habitat type (Proudfoot et al., 2020). The study of patch shape provides opportunities for novel scientific questions and investigations such as the implications of disturbance-induced habitat fragmentation. Destructive physical disturbances may lead to habitat fragmentation, with reduced patch size and increased exposure to edge effects, compromising the capacity to support the originally present assemblages. Through exposure to currents and turbidity, the habitat quality of trawled isolated patches of habitat-forming cold-water coral can decrease compared to undamaged cold-water coral habitat, and are therefore less likely to be recolonised by larvae over time, influencing population structuring (Harris, 2012a).

The suitability of spatial pattern metrics as a spatial proxy in ecological studies of biological assemblage structure has been demonstrated for deep seabed environments (Table 1.3). One such study found demersal fish assemblage structure was strongly influenced by the relative proximity and interspersion of benthic habitats into the broader seascape, in addition to focal habitat characteristics (Anderson et al., 2009). On the Rockall Bank, NE Atlantic, spatial composition and configuration of sediment characteristics measured in buffers around biological observations were strongly associated with morpho-species distribution (Robert et al., 2014) and were more important predictors of cold-water coral habitat than measures of terrain structure (Robert et al., 2016).

Measures of seascape composition and two-dimensional configuration applied to habitat maps also offer opportunities to explore patch dynamics, the changes in patch characteristics over space and time (Levin, 1992). The patch dynamics model predicts such changes influence habitat suitability, colonisation dynamics and ultimately population and metapopulation dynamics (Jackson et al., 2018). For example, a study from deep-sea benthos in the Pacific Ocean explicitly recognised the importance of patch dynamics, suggesting that fine-scale dynamic processes as patch extinction and

variability, competitive exclusion and variability in carbon supply influence species occurrence and coexistence (McClain et al., 2011). Patch dynamics can be incorporated into a pattern-oriented monitoring tool and has proved useful in terrestrial and shallow water change detection and quantifying multi-year changes in Antarctic benthic fauna's spatial patterning (Teixidó et al., 2002). The above examples demonstrate that patch representations are becoming a promising avenue to quantitatively explore the relationship between multiscale seascape composition and configuration, biodiversity patterns and resulting ecosystem processes. Further research could build on these early examples using patch metrics to study the effect of seascape composition and configuration on processes such as movement behaviour and to better understand the patch dynamics of benthic colonisation (Proudfoot et al., 2020).

Continuous seascape structure

In some cases, surface metrics are more appropriate metrics, or can be combined with patch metrics to capture a broader range of geometric features of the seascape. Continuous seascape structure refers to gradients in environmental conditions, such as terrain structure or habitat suitability, and can be quantified from terrain models or predictive distribution models. Multiscale terrain structure, represented in digital bathymetric models, includes variable gradients such as topographic complexity that may affect habitat suitability through its correlations with substratum quality for colonisation, niche space, refuge, hydrodynamic flow characteristics and nutrient deposition patterns (Pygas et al., 2020). That variations in terrain structure influence the occurrence and structuring of biological assemblages at the seabed has been demonstrated in multiple seabed environments, including in abyssal plains (Durden et al., 2015), continental margins (Jones & Brewer, 2012; Levin et al., 2010), banks and seamounts (Quattrini et al., 2017), and at finer spatial scales within cold-water coral reefs (Price et al., 2019). Quantitative measures of continuous seabed surface structure are now routinely applied as spatial predictors in DMs. However, spatial pattern metrics may also be applied to the mapped prediction to quantify the spatial structure in predicted biological distributions and ecological processes. For example,

predictive habitat suitability gradients can be used as spatial proxies for modelling processes such as movement behaviour or responses to changes in habitat suitability such as habitat fragmentation or loss of structural complexity (Pittman & Brown, 2011). Potential exists to use predicted species distribution patterns to examine the geography of functional traits and resulting ecological functions, such as developing spatial proxies for biologically mediated nutrient cycling (Snelgrove et al., 2018). Continuous gradient representations also offer opportunities to quantitatively explore and assess the effect of varying scales on ecological relationships. For example, terrain metrics extracted using moving windows of variable sizes helped identify the scale at which the relationship between cold-water coral diversity and terrain complexity was strongest (Price et al., 2019), and identify species-specific scale-dependent relationships using multi-scale models (Pittman & Brown, 2011). In seabed environments, DMs using continuous terrain metrics increasingly move beyond explanation and representation of biological patterns. DMs have been used to delineate essential fish habitat, conduct life stage studies and projections of habitat changes (Kenchington et al., 2019a), to study genetic variation and adaptation potential (Miller et al., 2019), to inform fisheries management (Stamoulis et al., 2018) and seascape connectivity conservation (Stuart et al., 2021).

Establishing guidelines for selecting patch and gradient metrics for ecological models and at what scale(s) to apply metrics remain important challenges for seascape ecology. Recognising that both patch-based and gradient spatial pattern metrics have ecologically relevant characteristics, seascape ecologists studying coral reefs have combined metrics from both spatial constructs to model, map and explain ecological associations finding that a combination of metric types best explains biological assemblages (Sekund & Pittman, 2017; Wedding et al., 2019). For the deep seabed too, the value of combining different representations has been demonstrated to study the driving factors of species distributions (Moore et al., 2011; Robert et al., 2014). Furthermore, it is also possible to create patch-based representations from the mapped outputs from geomorphometrics, for example, classes of low to high rugosity (Kågesten et al., 2019).

Seascape connectivity

Ecological connectivity is a central topic in landscape and seascape ecology and refers to the movement of populations, individuals, genes, gametes and propagules between populations, communities and ecosystems, as well as that of non-living material from one location to another (Hilty et al., 2020) (Fig. 1.5b). Connectivity is important for gene flow, maintaining healthy populations and metapopulations, and resilience of ecosystems and populations to disturbance events (Olds et al., 2016). Research into animal movements and genetic connectivity is of increasing interest in the deep-sea research community for its implications for marine conservation and ocean management, and has historically focused on cold-water coral, seamount and vent habitats (Taylor & Roterman, 2017). Deep-sea connectivity research largely draws on genetic approaches and numerical models of larval dispersal (Gary et al., 2020; Hilário et al., 2015). Challenges remain in identifying the mechanisms behind seabed population connectivity and their effects due to limited data availability on organism reproductive strategies and movement behaviour in the deep sea (Taylor & Roterman, 2017).

Few of the deep-sea studies of connectivity draw from landscape ecology and instead emerge conceptually from biological oceanography. However, there remains great potential to adapt approaches from landscape ecologists who often work with models and spatial proxies for variables where insufficient direct data are available. These include using structural connectivity as a proxy to predict actual connectivity pathways (Calabrese & Fagan, 2004; Kenchington et al., 2019b) and using graph-theoretic approaches such as network models (Treml & Kool, 2018). Connectivity metrics and models quantify ecological connectivity through a focus on either: 1) structural connectivity (i.e. an inference of seascape connectivity from the distribution and spatial properties of physical attributes of the seascape only (Meynecke et al., 2008; Weeks, 2017); 2) potential connectivity (i.e. inferring connectivity from seascape attributes combined with limited data on species mobility or dispersal capability (Proudfoot et al., 2020); or 3) actual connectivity (i.e. direct data on movement such as can be acquired with telemetry) (Pittman & McAlpine, 2003). Structural connectivity approaches consider the location, size, shape, and separation of habitats

as habitat fragmentation may predict population spatial dynamics and behaviour (Calabrese & Fagan, 2004). For example, structural connectivity approaches have successfully linked wetland connectivity to higher fish catch per unit effort, indicating connectivity between coastal habitats positively affects fish stocks (Meynecke et al., 2008). In the deep sea, structural connectivity approaches have demonstrated structural connectivity between 14 closed areas containing vulnerable deep-sea coral and sponge habitat in the North-West Atlantic (Kenchington et al., 2019b). Potential connectivity approaches incorporate species-specific dispersal capabilities or physical processes in the overlying water column that influence connectivity (Hilário et al., 2015) and their use in quantifying seabed structure can provide valuable outputs relevant for marine conservation (Proudfoot et al., 2020). Spatial patterns can be used as proxies to estimate the impact of seascape structure on animal movements. For example, in Newman Sound, eastern Canada, patch size and proximity were used as spatial proxies to model cost surfaces to lobster movement and inform conservation planning solutions (Proudfoot et al., 2020). Actual connectivity research in marine systems incorporates information on measured species-specific movements, such as the dispersal of larvae and post-settlement processes using genetic techniques, models and markers, further improving the functional relevance of the results (Baco et al., 2016). Even though major gaps remain in our knowledge of dispersal capacities of deep-sea species, our ability to track animal movements using technologies such as GPS tags, sensors and acoustic transmitters is increasing, as are capabilities to model animal movements and interpret genetic information (Harcourt et al., 2019). For example, microsatellite DNA revealed that seamounts can function as isolated islands or stepping stones for different taxa and reproductive strategies with implications for designing protected area networks (Miller & Gunasekera, 2017).

Connectivity research could also benefit from the application of individual-based models (IBMs). IBMs offer a bottom-up approach to explore the responses of individual organisms and ecosystem variables to simulations of different spatial configurations over a range of temporal and spatial scales (Hovel & Regan, 2018). Such experiments are relevant for seabed environments, where the possibility of in-situ manipulation of

seascape characteristics is limited. IBMs have been integrated with hydrodynamic models to simulate the supply of larvae to coastal nurseries (Rochette et al., 2012). Although IBMs are ideally constructed and validated using in-situ data on organism behaviour, they can prove useful when estimates are provided (Hovel and Regan, 2018). Because of the strong influence of hydrodynamic effects on species dispersal, benthopelagic coupling, vertical connectivity between benthic systems, and the influence of terrestrial and atmospheric processes on the deep sea present important focal areas for seascape connectivity studies. Further development of ecologically relevant pelagic spatial pattern metrics quantifying multiscale patchiness and gradients have been proposed to advance the study of vertical connectivity (Kavanaugh et al., 2016).

Context

Seascapes at any scale consist of a hierarchically structured assemblage of environmental conditions connected to, and influenced by, neighbouring environments – the seascape context (Figure 1.5c). Examples of broader contextual processes influencing the benthic environment include nutrient falls from higher water masses (whales, jellyfish) (Sweetman & Chapman, 2011), sediment deposition from land-based sources (Fontanier et al., 2018) or global heating of the ocean (Danovaro et al., 2020). At finer spatial scales, community characteristics of sediment infauna have been best explained by the characteristics and patch size of nearby cold-water coral reefs (Bourque & Demopoulos, 2018). Omitting consideration of spatial context in the study of the structural patterns of a single focal habitat type may therefore fail to elucidate all drivers of biological variation in focal patches and might limit model transferability (Bradley et al., 2020), which is particularly important for data-poor deep seabed environments.

As patch context influences focal-level processes, ecological models should include both patch variables and patch context. Seascape ecology studies in shallow coastal ecosystems have demonstrated the importance of considering patch context to explain structuring of coastal marine fauna (Bradley et al., 2020; Grober-Dunsmore et al., 2007). Similarly, patch context can likely improve our understanding of the influence of the surrounding environment in deep seabed focal patches. A hierarchical seabed

survey applying spatial pattern metrics at multiple scales to ROV imagery and sonar-derived data found that accounting for the surrounding (30 m and 75 m) spatial context of sediment patches almost doubled the explanatory power of models of variability in morphospecies composition and biodiversity across the Rockall Bank, NE Atlantic (Robert et al., 2014). Likewise, broad- (kms) and fine (1–10s of m) scale demersal fish-seabed habitat associations were found to be strongly dependent on habitat context, and zones close to multiple distinct habitat types contained distinct fish assemblages (Anderson et al., 2009).

Scale

The processes responsible for environmental heterogeneity operate across temporal and spatial scales, and individuals, life-stages, species and communities respond to habitat patterning differently across these scales (Martin, 2018; Turner & Gardner, 2015; Wiens, 1989). The concept of scale covers two aspects: resolution and extent, which can be both temporal and spatial. Secondly, scale consists of a thematic scale (i.e. the number of habitat classes and how they are defined), an ecological scale (i.e. scale of a phenomenon), an observational scale (i.e. the scale at which data is collected) and an analytical scale (i.e. the scale at which data on the phenomenon is analysed). The selection of spatial and temporal extent(s) and resolution(s) can therefore have profound implications for the capability to successfully link pattern to process (Kendall et al., 2011; Lecours et al., 2015; Levin, 1992; Wu, 2004), as mismatches between ecological scale, observational scale and analytical scale might compromise the ability to define biota-environment relationships accurately (Holland et al., 2004). The challenge of linking spatial patterns to ecological processes over multiple scales and identifying the most influential scales (scale of effect) has been and continues to be a focal area of landscape ecology (Levin, 1992; Martin, 2018; Wiens, 1989).

Temporal and spatial dynamics are challenging to capture in the deep sea, as few research programmes can afford to survey the same area over multiple spatial and temporal scales (Woodall et al., 2018). As such, seascapes are often defined at arbitrary scales based on data availability, convenience, or a single conventional

sample unit area increasing the risk of a scale mismatch (Lecours et al., 2015; Pittman & McAlpine, 2003). Although conventional habitat maps are static representations, seabed structure, especially soft bottom sediment, can be relatively dynamic over temporal and spatial scales with consequences for multiscale biodiversity patterns (Zajac et al., 2013). For example, responses of macrofaunal benthos to seabed habitat heterogeneity are strongly scale-dependent. In soft-sediment environments in Monterey Canyon, faunal turnover changes were linked to scales of geographic canyon features (McClain & Barry, 2010). At the topographically complex seabed of the Mauritanian slope, megafaunal composition differed between broad-scale geomorphological features but exhibited limited fine-scale variability (Jones & Brewer, 2012).

Landscape ecology has explored the consequences of scale more than any other ecological science and provides an evidence base and analytical tools (Huais, 2018; Jung, 2016) to address key questions about scale effects and guide scale selection (McGarigal et al., 2016; Wiens, 1989). Exploring scale effects requires a multiscale approach, for example, using analytical windows of various dimensions. This is particularly important in the absence of any evidence to select a specific focal scale or set of analytical scales. A study in the Clarion-Clipperton zone evaluating increasing megafaunal sample area confirmed that spatial tuning of sampling units helped infer reliable ecological relationships in abyssal environments, where faunal density is typically low (Simon-Lledó et al., 2019). When employing a single scale, a minimum requirement to successfully link pattern to process is that the ecological phenomenon under consideration falls within the observational and analytical scales selected for the research (Hobbs, 2003; Wiens, 1989). Based on hierarchy theory, seascape approaches advocate a hierarchical scaling concept where a focal scale or ecological neighbourhood (anchored in time and space to a defined phenomenon) is nested between a set of broader scale variables and a set of finer-scale variables (Pittman & McAlpine, 2003; Pittman et al., 2004). Such hierarchical approaches can provide an organising framework to explore scale effects and help identify the most appropriate scale of analysis and response for the phenomenon under consideration (Kavanaugh et al., 2014; Porskamp et al., 2018). In map production, hierarchical approaches have been employed in several seabed habitat

classification schemes such as the European Nature Information System (EUNIS) and the Coastal and Marine Ecological Classification Standard (CMECS) in the United States designed to capture different levels of heterogeneity for different applications (Harris, 2012a). As the technological advancement of data acquisition and analysis techniques continues, sampling over multiple spatial scales and explicit consideration of scale dependencies and appropriateness of scales applied in ecological analyses remain important focal areas in seabed research (Lecours et al., 2015).

1.2.6 Informing ecosystem-based conservation of the deep seabed

Policy targets around sustainable use of the ocean, such as Aichi Biodiversity Target 11 and UN Sustainable Development Goal 14, advocate ecosystem approaches for biodiversity conservation (Rees et al., 2018). These recognise landscape ecology concepts related to seascape structure, connectivity and context (e.g. habitat size and quality, habitat diversity and representation, ecological connectivity, fragmentation) as important design and evaluation criteria for area-based management tools (Crowder & Norse, 2008; Pittman et al., 2021). Top-down habitat maps are the most commonly applied strategy to identify priority areas of seabed for management planning and have become a key information source to guide and evaluate the size and shape of marine protected areas and the spatial configuration of MPA networks in the deep sea (e.g. Hogg et al. 2018). Informing the science-based design of ecologically relevant MPAs for deep seabed environments is complicated by the limited availability of high-resolution data, and considerable knowledge gaps exist when attempting to scale up information from a few detailed study areas and when linking seascape structure to ecosystem processes. It is here that the multiscale and pattern-oriented framework developed in seascape ecology can help integrate existing data and generate new data and understanding to support operational decision making in ecosystem-based management (Young et al., 2018).

MPA design

Designing effective MPAs and networks of MPAs that address ecological coherence criteria requires spatially explicit knowledge of biodiversity distributions and the link

between seabed patterning and ecological functions, including ecological connectivity (Young et al., 2018). Seascape ecology concepts and techniques have been used to inform and evaluate MPA design using pattern-derived proxies of seascape composition, configuration, connectivity and context (Hilário et al., 2015; Huntington et al., 2010; Young et al., 2018). Integrating habitat maps and spatial pattern metrics, the size, location and shape of an MPA or network can be designed to include spatial targets for habitat representativity, replication and redundancy, to prioritise certain seascape configurations, protect ecological corridors, or specific attributes such as to maximise or minimise edge effects (Huntington et al., 2010).

Seascape ecology within a systematic conservation planning framework has considerable potential to derive spatial recommendations for MPA network design. For example, incorporating spatial information on biophysical gradients and other ecologically important features with seascape ecology principles helped design a proposal for an MPA network safeguarding biodiversity and ecosystem function in the Clarion–Clipperton Fracture Zone (CCZ) (Wedding et al., 2013). The connectivity of deep-sea populations is increasingly recognised as a priority research area for the establishment of such MPA networks, as disturbances to population connectivity (e.g. mining plumes) can impact their persistence as well as the effectiveness of protection measures (Danovaro et al., 2020; Howell et al., 2020; O'Leary & Roberts, 2018). Since actual connectivity patterns for deep-sea species are often unavailable (Baco et al., 2016; Hilário et al., 2015), seascape ecology-based structural and potential connectivity metrics and spatial models such as IBMs and graph-theoretic approaches (Treml & Kool, 2018) incorporating seascape configuration could be increasingly important for seabed connectivity analysis. For example, the implications of seascape configuration have helped to evaluate functional connectivity to promote spatial resilience, productivity and recovery between high seas MPAs containing fragmented deep-sea populations (Kenchington et al., 2019b). Knowledge of such pathways may further inform the establishment of blue corridors that enhance seascape connectivity for ecologically coherent MPA networks (Hopkins et al., 2020).

When focusing on ecological functions, rates of ecological processes such as carbon storage may vary as a function of biological patterning (Asplund et al., 2021). Understanding linkages between such biological seascape patterns might help understand spatial variation in carbon sequestration and storage across the deep seabed (Snelgrove et al., 2018)and help identify priority regions for conservation measures. Additionally, considering the wider geographical context of MPAs and MPA networks is necessary for their ecological coherence. This includes the multiscale characteristics of surrounding environments, external drivers and anthropogenic disturbances that may affect patterns and processes within the MPA location under consideration (Hopkins et al., 2020). Such interactions of external and internal components are typically non-linear and can result in unexpected emergent properties that can influence the effectiveness of management approaches developed on exclusive consideration of one focal seascape (Peters et al., 2007). Buffer zones, for example, have been proposed to protect seabed MPAs from contextual disturbance effects as mining plumes (Wedding et al., 2013). Building on these principles, spatial pattern metrics may also be used to assess whether proposed or existing MPAs are meeting science-based MPA design principles. For example, a seascape ecology methodological framework successfully evaluated whether the design of the Central Coast MPA Network in California met management goals for habitat replication and representation, biological diversity, and the reduction of spill-over into adjacent fishing grounds (Young et al., 2018). In the High Seas, habitat maps combined with seascape ecology principles in systematic conservation planning have been used to assess the efficiency and representativeness of the existing MPA networks in the Northeast Atlantic, finding that the network was not the most optimal solution (Evans et al., 2015).

Monitoring seascape dynamics

As seascapes are dynamic and changes to seascape composition and configuration can affect ecological processes, an improved understanding of the drivers and the dynamic spatio-temporal character of these changes can help predict how the system will respond to stressors (Turner, 2005). Spatial pattern metrics can provide a useful

approach for monitoring seascape change, comparing different seascapes, or conducting impact assessments (Wedding et al., 2011). In monitoring, spatial pattern metrics have successfully been applied to assess changes in benthic community structure (Teixidó et al., 2002) and may also be applied to inform sampling design and targeted monitoring strategies, for example to target a specific functionally relevant mosaic of patch types or a specific spatial configuration (Pittman et al., 2007). Spatial pattern metrics also have potential to quantitatively compare seascapes and evaluate how different seascape structure effects key ecological processes such as MPA rates of recovery, spatial resilience and the provisioning of ecosystem services of interest to management. When interested in impact assessments, spatial pattern metrics may be applied to quantify and monitor the structural effects of disturbances, for example resulting from impacts of mining and trawling (Danovaro et al., 2020), on biodiversity, ecological functions, and recovery potential. For example, Teixidó et al. (2007) applied spatial pattern metrics to quantitatively describe the patterns of recovery of Antarctic benthic communities after iceberg scouring, and found that benthic cover area was the best predictor of recovery.

1.2.7 Summary and outlook

As geospatial technology advances and data availability increases for the global deep sea, together with a demand for knowledge at scales relevant to policy and management decision making, the interest in a seascape ecology framework for the seabed is likely to grow. This review highlighted with examples how the application of spatial pattern metrics at multiple scales enables a quantitative exploration of seascape heterogeneity and its consequences on ecological patterns and processes through concepts as seascape composition, configuration, terrain structure and connectivity, whilst considering the roles of context and scale. This spatially explicit, pattern-oriented approach can help address knowledge gaps around drivers and implications of spatial structure, scale dependency and hierarchical cross-scale interactions. This may also result in insights operationally relevant to addressing real-world conservation and management challenges, such as conservation prioritisation, protected area network design and monitoring of ecological change and disturbance effects. However, examples also

demonstrate that applications in deep benthic seascapes are limited and differ strongly in target system and spatial scale. To facilitate the transition of seascape ecology to applications in deeper benthic terrains, more empirical investigations of seascape environmental heterogeneity, focusing on key conceptual areas, will help seascape ecology reach its potential in addressing the multiscale and dynamic relationships between seabed patterns and ecology.

1.3 Objectives

The review highlighted several focal areas that would benefit seabed and habitat heterogeneity research and enable the transition of seascape ecology to the deep seabed. The objectives of this thesis relate to the application and ecological relevance of spatial pattern metrics at the seabed, which can be divided in three main themes:

1. To test spatial pattern metrics as methodology to represent seabed seascape structure

    (a) To assess the potential of patch-based metrics from categorical seabed habitat maps *to quantitatively describe seascape structure*

    (b) To assess the potential of patch-based metrics as an option *to compare* seascapes and associated communities

2. To test the ecological relevance of spatial pattern metrics quantifying deep seabed structure

    (a) To assess the utility of *patch-based metrics* quantified from categorical habitat maps *to explain and predict* biological patterns

    (b) To advance the application of *surface metrics, DMs and their outputs* to predict biological patterns and processes

    (c) To *combine patch-based and terrain metrics* to explore the effect of heterogeneity in seascape structure on biodiversity, and identify relevant predictor variables

3. To apply spatial pattern metrics and concepts to support applied seabed management research

   (a) To include *multi-scale spatial data and geographical context* to determine scale dependency and cross-scale interactions on biodiversity characteristics

   (b) To apply seascape ecology concepts and analytical techniques to support *identification of ecologically important features and biodiversity areas* in the deep sea

These objectives will be addressed using case studies focusing on ecological hypotheses relevant to seamounts and atoll slopes in the Western Indian Ocean (WIO). Seamounts and atoll slopes hosting deeper reef (∼30 m-300 m depth) ecosystems are appropriate study systems because of their high multi-scale environmental heterogeneity in patch-mosaic and terrain structure along the depth gradient. To date they are challenging environments to study, despite their importance. Therefore, many knowledge gaps remain about how heterogeneity in spatial structure supports these high levels of biodiversity on seamounts and atoll slopes. Elucidating the character of seabed and habitat heterogeneity, and the potential of spatial heterogeneity represented as patch-mosaic or continuous terrain to function as a proxy for biodiversity in these systems will therefore form the focus of objectives.

1.4 Case study details

1.4.1 Study area and systems

The WIO (Comoros, French overseas territories, Kenya, Madagascar, Mauritius, Mozambique, Seychelles, Somalia, South Africa, and Tanzania) covers approximately 30 million km^2 or 8.1% of our global ocean (Obura et al., 2017). Its marine (e.g. fish life) and coastal biodiversity (e.g. mangroves, seagrasses, tropical coral reefs) provide important benefits to a population of about 220 million. Some 60 million people live within 100km of the shoreline, with cultures and traditional livelihoods

inextricably linked with functional ecosystems supporting fisheries and maritime trade (Obura et al., 2017).

Despite the importance of the marine environment for the inhabitants of the WIO, the provisioning of marine resources and food security is increasingly threatened by impacts from resource exploitation, anthropogenic habitat degradation, population growth, pollution and climate change (Obura et al., 2017). Effective management of ocean assets is necessary to maintain resilient marine ecosystems and, by extension, ocean-dependent economies. Protecting the functions of marine ecosystems requires knowledge of the multiscale environmental characteristics that support biodiversity and ecological processes across the depth gradient (Crowder & Norse, 2008). However, the Indian Ocean is amongst the least studied oceans (Stefanoudis et al., 2020) and access barriers to scientific assets to research coastal and marine environments at depths beyond 30 m, further limit the availability of knowledge to address current challenges (Woodall et al., 2021). By extension, available data on seamounts and atoll slopes hosting deeper reef ecosystems are limited and dispersed. Yet, both systems support valuable biodiversity and fisheries resources, and are an important priority for conservation management (Maina et al., 2020; Tyler et al., 2009).

Seamounts

Seamounts are elevated rises of the seabed and are recognised as some of the most prominent and widespread features of seabed topography. Although they are defined as having an elevation > 1000 m, the term 'seamount' is also readily used for features of lower elevations (> 100 m) in ecology (Wessel, 2007). The lack of high-resolution seabed data limits our exploration of seamounts, including counts of their abundance (Watts, 2019). Using satellite altimetry at 30 arc seconds it has been estimated that there are over 33,000 large (> 1000 m) seamounts (Yesson et al., 2011), but the number of smaller seamounts (>100 m) that cannot be detected using this method may be much higher (Hillier & Watts, 2007). Most of these are of volcanic origin and are found on plate boundaries such as mid-ocean ridges, faults and island arcs, but their abundance varies among ocean basins (Wessel, 2007).

Highly heterogeneous in geomorphology and hydrographic phenomena, seamounts act as biodiversity hotspots (Rowden et al., 2010). They are associated with distinct benthic communities, such as cold-water corals composing Vulnerable Marine Ecosystems (VMEs), that create habitat for associated fauna (Buhl-Mortensen et al., 2010). Local currents drive upwelling around the seamounts, which may enhance primary productivity supporting pelagic species, including species important for fisheries, seabirds and marine mammals White et al. (2008). As seamounts often support large aggregations of commercially important fish species, they have become increasingly subjected to extensive bottom trawling (Clark et al., 2010). Trawling damages bottom structure and as many benthic ecosystem components have slow growth rates, their potential to recover from such impacts is limited (Williams et al., 2020, 2010). Likewise, the life history traits of targeted deep-sea fish species make some especially vulnerable to overfishing (Clark, 2001). Older seamounts can accumulate important mineral deposits (i.e. cobalt crusts) and are now of interest to the seabed mining sector (Clark et al., 2012). Although commercial mining has not yet taken place, impacts of drilling and dredging on seamount communities are expected to be significant (Rogers, 2018).

Conservation and management of seamounts is hampered by a lack of data and challenges of high sea legislation (Morato et al., 2010; Rogers, 2018). The inaccessibility and costs of research on deep-sea ecosystems as seamounts means most studies are based within the national jurisdictions of countries with large research budgets (Danovaro et al., 2020). Yet, most seamounts exist in Areas Beyond National Jurisdiction (ABNJ) (Taranto et al., 2012). As any nation can access fisheries resources in ABNJ, these areas increasingly receive attention at international policy level to construct legal frameworks to protect vulnerable ecosystems as seamounts (Ban et al., 2014; Dunstan et al., 2016). Until this is achieved, regional initiatives and intergovernmental bodies that regulate fishing, mining and shipping form critical initiatives to protect habitats in ABNJ (Wagner et al., 2020).

Seamounts along the Southwest Indian Ridge (SWIR), an ultra-slow spreading divergent plate boundary between the African and Antarctic plates, remain amongst the most poorly studied globally, particularly in terms of their ecology (Rogers et al.

2017). Despite the limited information available, some SWIR seamounts have become established as Ecologically or Biologically Significant Marine Area (EBSAs) (Convention on Biological Diversity, 2015a,b). SWIR seamounts host valuable marine resources. Demersal and bentho-pelagic fish have been trawled since the 1970s and some seamounts may host polymetallic sulphides (Marsac et al., 2020). Governance to mitigate these and future impacts is lacking, although the Southern Indian Ocean Deepsea Fishers Association (SIODFA) has made some progress in implementing voluntary conservation and management measures focusing on benthic protected areas (Marsac et al., 2020).

Oceanic islands and deeper reefs

Like seamounts, oceanic islands are topographic elevations rising from the seafloor but penetrate the sea surface. They often form part of larger chains, but have never been connected to the mainland (Dawson, 2016). Their slopes provide a variety of habitats resulting from heterogeneity in topography, size, age, oceanographic processes, gradients in water chemistry, nutrient availability and isolation (Quimbayo et al., 2019). Coral reefs may form on oceanic islands within 30° of latitude from the equator, and can ultimately lead to the formation of an atoll providing the framework for a barrier reef enclosing an open lagoon (Floyd, 1991).

The coral reefs associated with oceanic islands host distinct biodiversity and may extend to light-limited depths in clear tropical and subtropical waters. Between 30-150 m, these deeper reefs form mesophotic coral ecosystems (MCEs) (Hinderstein et al., 2010), and rariphotic systems extend to 300 m depth (Baldwin et al., 2018). Deeper reefs in the mesophotic and rariphotic zone have long been considered 'too deep' for shallow water coral researchers ($<$ 30 m depth), and 'too shallow' for deep sea ($>$ 200 m depth) ecologists, and scientific research on deeper reefs has only truly accelerated since 2010 (Bongaerts et al., 2019). Deeper reefs host biodiverse communities (Lesser et al., 2018), may function as possible refugia or source for shallow-water reef species (Bongaerts et al., 2010; Lesser et al., 2009), form essential fish habitat (Blyth-Skyrme et al., 2013), provide key ecosystem services (Holstein et al., 2019) and meet the criteria to be classified as Ecologically or Biologically Significant Marine Areas (EBSAs)

(Soares et al., 2020). Although their depth shelters deeper reefs from some of the stresses shallow water reefs experience, threats such as overfishing (Lindfield et al., 2016), invasive species (Andradi-Brown et al., 2017), coastal development and runoff from land (Appeldoorn et al., 2016), pollution, resource exploration activities and the consequences of climate change may nevertheless affect their health and persistence (Holstein et al., 2019; Rocha et al., 2018).

Although deeper reef research is increasing globally, particularly in the mesophotic zone (Loya et al., 2016), widespread knowledge remains limited by the need for specialised equipment, technology and training (Armstrong et al., 2019). Detailed characterisations of deeper reefs remain rare compared to shallow water reefs (SWRs) and often carry a geographic bias with most studies conducted in Caribbean, Australian and increasingly US Pacific waters (Turner et al., 2017). Biological occurrence and distribution data for deeper reefs are unavailable for many parts of the WIO (Pyle & Copus, 2019), despite the possible abundance of these systems in the region (Goldberg, 2016; Stoddart, 1973; Wagner et al., 2020). Knowledge of the environmental drivers and distribution of deeper reefs in the WIO might further help to define priority features for deeper reef conservation and ecosystem-based management (Turner et al., 2019), with currently few specific conservation efforts targeting deeper reefs in this region (Stefanoudis et al., 2022).

1.4.2 Data collection

Datasets from two locations (Fig. 1.6a) were used in this thesis to address knowledge gaps on the roles of environmental heterogeneity as driver of seamount and deeper reef biodiversity in the WIO. Data on the SWIR seamounts were collected by cruise JC066 aboard the RSS *James Cook* in 2011 (Rogers & Taylor, 2012). This NERC cruise focused on documenting and recording the benthic ecology of five seamounts: Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Bank and Atlantis Bank (Fig. 1.6c). This cruise was a sequel to the 2009 Fridtjof Nansen cruise which focused on investigating the pelagic biology around these seamounts (Rogers et al., 2017).

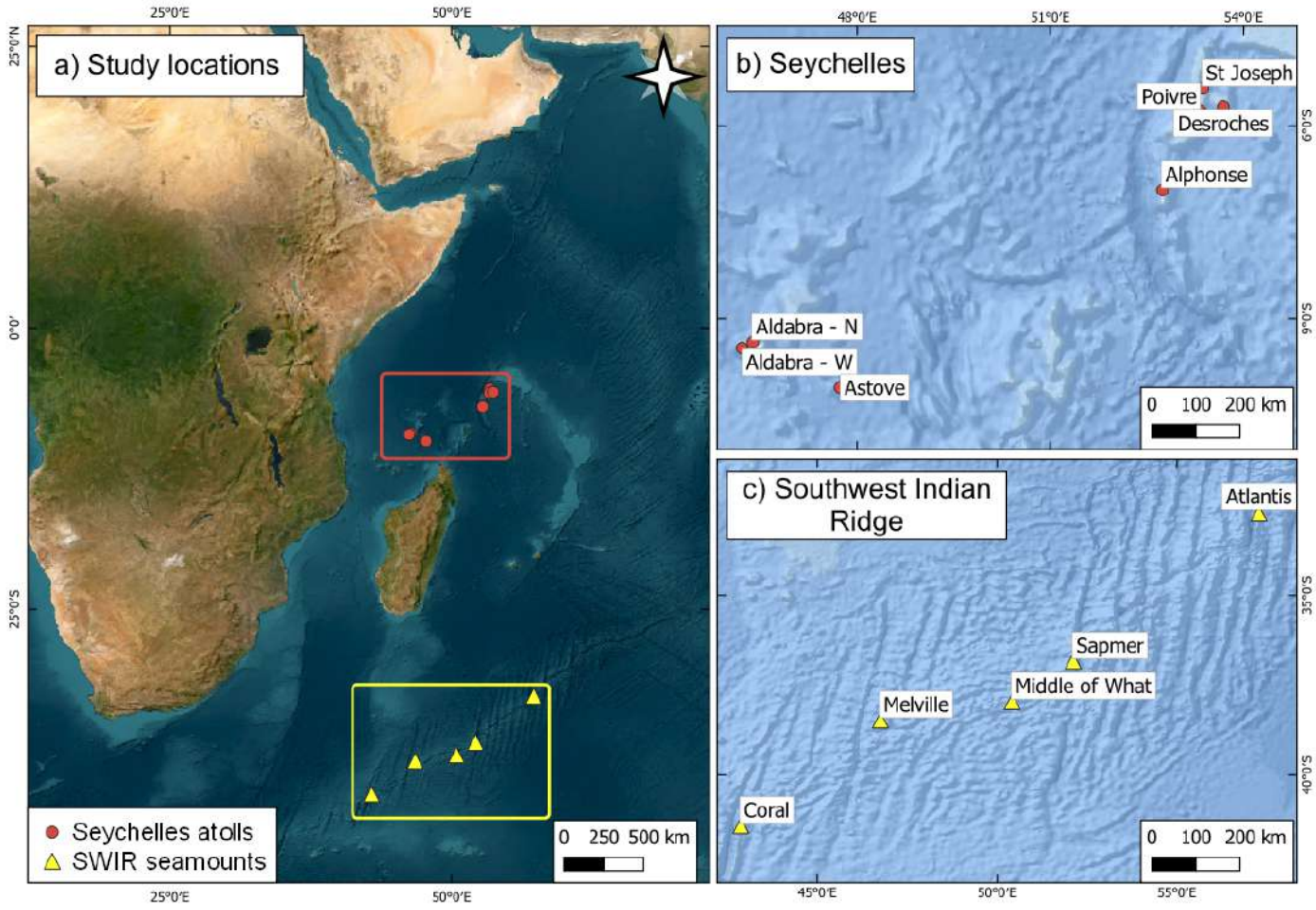


Figure 1.6: Research sites in the Western Indian Ocean (a): atolls in Seychelles (b) and seamounts along the Southwest Indian Ridge (c)

During this expedition a large variety of environmental and biological datasets were collected. Environmental data used in this thesis to describe seabed spatial heterogeneity of each seamount were swath bathymetry and backscatter data acquired using a hull-mounted Kongsberg-Simrad EM120 multibeam echosounder. Ground truthing data to link environmental structure to biodiversity were collected using upslope vertical video surveys with the ROV Kiel 6000. The ROV also carried a CTD for in-situ data collection on oceanographic parameters. Data on deeper reefs along atoll slopes was collected during Seychelles: First Descent in 2019 aboard the Ocean Zephyr, which was a scientific expedition co-produced with the Seychelles Government, Partners and Nekton (Woodall & Rivers, 2019). The expedition aimed to contribute to a baseline of marine life to 500 m deep in the Indian Ocean. During this cruise

data were collected on mesophotic and rariphotic ecosystems at seven sites around six coral atolls in Seychelles (Fig. 1.6b), which are also thought to provide a good study system for the wider region (Woodall & Rivers, 2019).

A subset of the environmental and biological datasets collected during this expedition was used used. Environmental data to describe seabed structure were collected as swath bathymetry and backscatter with a Teledyne Reson Extended range SeaBat T50-P from a workboat. Video transects collected using a human-occupied submersible (Triton 1000/2) or ROV (OceanModules V8 M500) were another source of environmental data and formed inputs for orthomosaics and digital elevation models produced using SfM photogrammetry. The main aim of the video surveys, however, was to collect information on biological communities at four different depths (30 m, 60 m, 120 m and 250 m).

1.5 Thesis structure and hypotheses

Described datasets were used to analyse the relationship between seabed heterogeneity and biodiversity in seamounts (Ch2 and 3) and deeper reefs (Ch4 and 5) (Fig. 1.7). The aims, hypotheses and methodology of each of the data chapters are briefly outlined below. Cross-cutting these case studies are the objectives stated in section 1.3 (Table 1.4). The case studies vary strongly in observational scale, analytical scale and the amount of ground-truthing data available for map production. They also demonstrate that what is considered a seascape, class or patch is strongly dependent on the question under consideration and scale of observation (Table 1.5).

Chapter 2: "Mapping, quantifying and comparing seascape heterogeneity at SWIR seamounts"

Although seamounts are often conceptualised as similar entities, they are highly variable in morphology with implications for the habitats and communities they support. Despite its ecological importance, environmental heterogeneity is rarely quantitatively studied in deep sea features such as seamounts which limits insights into spatial characteristics

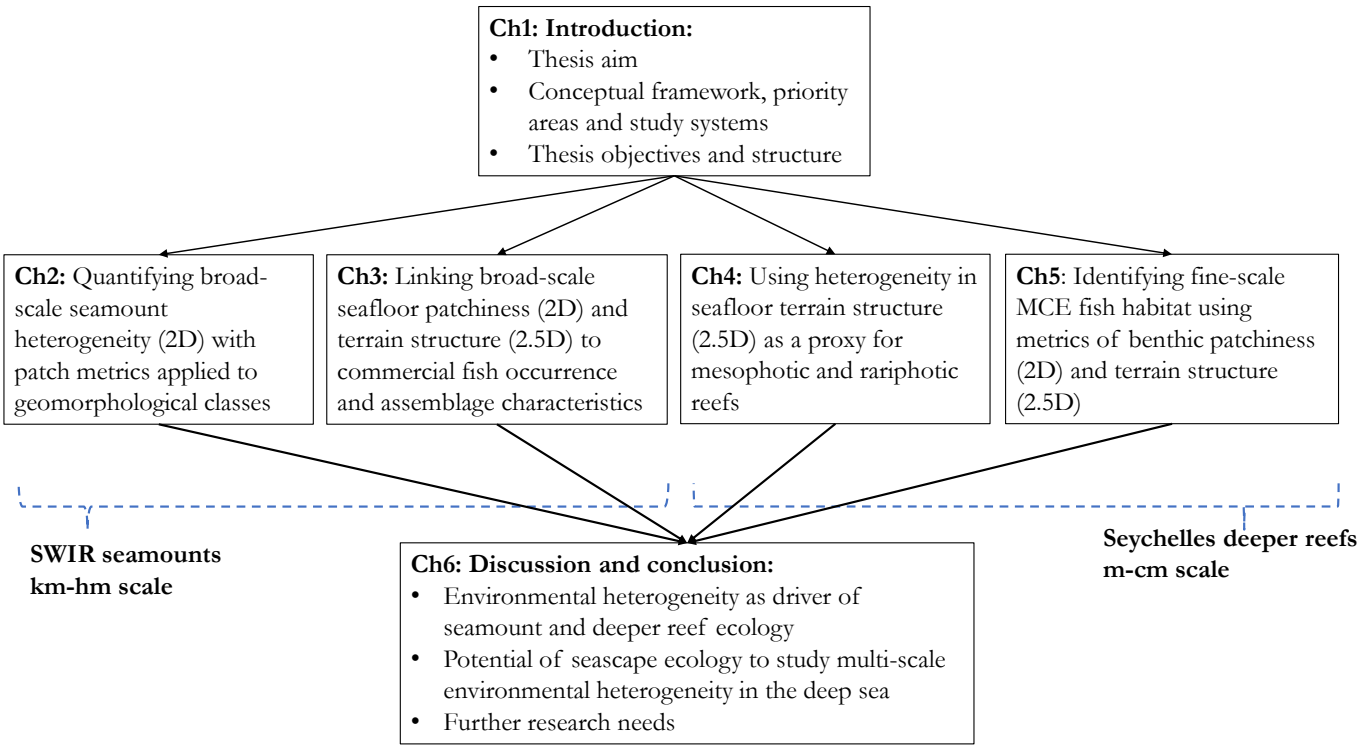


Figure 1.7: Thesis overview. Case studies on seamounts and deeper reefs used different spatial pattern metrics from seascape ecology to explore the character and consequences of seabed spatial heterogeneity. Case studies also strongly differed in scale of observation and analysis, ranging from kilometers (seamounts) to centimeters (mesophotic reefs).

relevant for representational ecosystem-based management. This study demonstrated a technique that applied spatial pattern metrics from seascape ecology to habitat maps created through unsupervised techniques at five seamounts to quantify and compare seamount seascape heterogeneity.

The hypothesis tested was that seamounts will vary in seascape composition and configuration because of their variable geomorphology. Theoretical implications of documented variance were also explored.

Chapter 3: "Seamount heterogeneity influences commercially important fish"

Seamounts attract high abundances and diversity of fishes, but knowledge gaps remain on the ecological importance of within-seamount habitat heterogeneity for demersal fish family occurrence, abundance, richness and diversity at these features. Environmental heterogeneity in the form of terrain structure, seascape composition and configuration

Table 1.4: Overview of main objectives addressed in each chapter

	Seamounts		**Deeper Reefs**	
	Ch2	Ch3	Ch4	Ch5
1: To test spatial pattern metrics to represent deep seabed seascape structure				
Objective 1a: To assess the potential of patch based metrics from categorical habitat maps to describe seabed structure	x	x		x
Objective 1b: To assess the potential of patch-based metrics to compare seascapes and associated communities	x			
2: To test the ecological relevance of spatial pattern metrics in the deep sea				
Objective 2a: To assess the utility of patch-based metrics quantified from categorical habitat maps to explain and predict biological patterns		x		x
Objective 2b: To advance the application of terrain metrics, DMs and their outputs to predict biological patterns and processes		x	x	x
Objective 2c: To assess the utility of combinations of patch-based and terrain metrics to explore the effect of heterogeneity in seascape structure on biodiversity, and identify relevant predictor variables		x		x
3: To support applied seabed management research with concepts and metrics				
Objective 3a: To include multi-scale spatial data and geographical context to determine scale dependency and cross-scale interactions on biodiversity characteristics	x	x	x	x
Objective 3b: To apply seascape ecology concepts and analytical techniques to support prioritisation of important habitat for deeper reef ecosystems and seamount communities		x	x	x

likely influences the movements of seamount-associated fish, and in turn ecological processes. This study investigated the combined effect of seascape composition and configuration measured using habitat maps produced in Chapter 2 and continuous terrain structure on commercially important demersal fish families at Coral seamount, Melville bank and Atlantis bank.

Hypotheses tested were that: a) specific fish families are associated with particular patch types corresponding to habitat preferences; b) more complex patch shapes will

negatively influence fish abundance, richness and diversity because of edge effects; c) larger patch sizes will positively influence fish abundance and richness as a result of species-area relationships; d) more aggregated seascapes will host increased abundance and richness because of structural connectivity between patch types; e) the responses of fish to environmental heterogeneity will be mediated by seamount site and depth, which are key drivers of seamount biodiversity.

Chapter 4: "Geomorphological drivers of mesophotic coral ecosystems around Seychelles"

Mesophotic (30-150 m) and rariphotic (150-300 m) deeper reef habitats are important from an ecological and conservation perspective, yet remain understudied. Key knowledge gaps exist on the environmental patterns and processes that drive and shape their geographical distributions. This study aimed to determine if seabed terrain structure quantified at multiple scales can act as a reliable spatial proxy for predicting deeper reef assemblage distribution. Using spatial predictive models, this study identified relationships between multiscale seafloor geomorphology and sessile benthic assemblages identified from video surveys in four atoll seascapes in Seychelles.

Hypotheses tested were that a) deeper reef biodiversity consists of vertically separated assemblages as a result of large environmental changes along the depth gradient; b) identified assemblages will be associated with unique combinations of geomorphological parameters – their environmental niche; and c) the importance and effect of predictors varies as a function of scale.

Chapter 5: "Structure-from-Motion photogrammetry demonstrates that multiscale seascape heterogeneity is essential in shaping mesophotic fish assemblages"

Tropical mesophotic coral ecosystems (MCEs) provide habitat for diverse fish assemblages, but the effect of multiscale spatial habitat characteristics on MCE fish assemblages is not well understood. To investigate the influence of benthic seascape structure on MCE fish assemblages in Seychelles, this study surveyed fish assemblages along the depth gradient using submersible video transects. Spatial pattern metrics

(composition, spatial configuration and terrain structure) were extracted from transect terrain models and orthomosaics produced with Structure-from-Motion (SfM) photogrammetry to quantify benthic spatial structure at cm-scale.

Hypotheses tested were that a) a combination of habitat composition, configuration and terrain structure is most appropriate to explain the hierarchical structuring of fish assemblages, as reef fish respond both to substratum patchiness and terrain structure; b) the importance of spatial pattern metrics will depend on geographic context and depth zone, as different areas will host varying assemblages with varying fine-scale habitat preferences; however, c) fine-scale terrain structure will positively influence fish biodiversity across mesophotic depths, following similar findings in shallow reefs and cold-water coral reefs.

Table 1.5: Overview of main seascape ecology concepts as applied in each case study, influenced by scales of observation and the question under consideration.

Concept	**Definition**	**Chapter interpretation**	**Extent and resolution**
Seascape	Spatially heterogeneous environments that can be delineated at a range of temporal and spatial scales	Ch2: entire seamount Ch3: 500 m buffer zones around transect Ch4: atoll slopes Ch5: individual transect	100s km^2, 25m ~1.2 km^2, 25m 2-4 km^2, 2m 250 m^2, 10cm
Class or patch type	Distinct units within the seascape with comparable environmental characteristics, e.g. substrate or habitat types	Ch2 and Ch3: mapped geomorphological class (slope, summit, NW or SE flank, ridge) Ch4: NA (analysis based on terrain metrics) Ch5: substratum type in transect (coral, sediment, macroalgae/seagrass, coral rubble, bedrock, sponges)	10s km^2, 25m) m^2 - 10s cm^2, 10cm
Patch	Area with internally homogeneous environmental conditions	Ch2 and Ch3: individual occurrence of each geomorphological class Ch4: NA (analysis based on terrain metrics) Ch5: individual occurrence of substratum class	100s m^2, 25m m^2 - 10s cm^2, 10cm

Chapter 6: "Discussion and conclusion"

The final chapter provides a synthesis of the contributions of this thesis to the development and applicability of seascape ecology in deep seabed environments following

the objectives listed in section 1.3. This synthesis includes novel findings on the ecologically relevant aspects of environmental heterogeneity of seamounts and deeper reefs and implications for conservation management at the WIO. Both aspects are used to suggest recommendations for further research to enhance the theoretical development of the field.

1.6 Publications resulting from this thesis

The following manuscripts from this thesis have been published:

- Denise Swanborn, Veerle Huvenne, Simon Pittman and Lucy Woodall (2022). Bringing seascape ecology to the seabed: a review and framework for its application. *Limnology and Oceanography.* 67, 1, 66-88. https://doi.org/10.1002/lno.11976 (Literature Review in Chapter 1).

- Denise Swanborn, Veerle Huvenne, Simon Pittman, Alex Rogers, Michelle Taylor and Lucy Woodall (2022). Mapping, quantifying and comparing seascape heterogeneity of Southwest Indian Ridge seamounts. *Landscape Ecology.* https://doi.org/10.1007/s10980-022-01541-6. (Data chapter 2).

- Denise Swanborn, Veerle Huvenne, Thomas Malpas, Simon Pittman, Alex Rogers, Michelle Taylor and Lucy Woodall. Seamount seascape composition and configuration shape Southwest Indian Ridge fish assemblages. *Deep Sea Research Part I: Oceanographic Research Papers.* https://doi.org/10.1016/j.dsr.2022.103921 (Data chapter 3).

- Denise Swanborn, Nico Fassbender, Veerle Huvenne, Simon Pittman, Paris Stefanoudis and Lucy Woodall (2022). Geomorphological drivers of deeper reef habitats around Seychelles. *Coral Reefs*, 41, 101-1006. https://doi.org/10.1007/s00338-022-02281-4 (Data chapter 4)

- Denise Swanborn, Paris Stefanoudis, Veerle Huvenne, Simon Pittman and Lucy Woodall (2022). Structure-from-Motion photogrammetry demonstrates that fine-scale seascape heterogeneity is essential in shaping mesophotic fish assemblages.

Remote Sensing in Ecology and Conservation. https://doi.org/10.1002/rse2.290 (Data chapter 5).

Published articles have been included in Appendix E.

Work conducted as part of this thesis has additionally formed input for the following published or submitted publications:

- Stefanoudis et al. (2022). Stakeholder-derived recommendations and actions to support deep-reef conservation in the Western Indian Ocean. *Conservation Letters*. 00, e12924. https://doi.org/10.1111/conl.12924
- Stefanoudis et al. (in review). *Trait-based approaches reveal that deeper reef ecosystems in the Western Indian Ocean are functionally distinct*. Proceedings of the Royal Society B.

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2 Quantifying and comparing spatial heterogeneity of Southwest Indian Ridge seamounts

Abstract

Seamounts are widespread geomorphological features creating seabed spatial heterogeneity, a main driver of deep-sea biodiversity. Despite its ecological importance, substantial knowledge gaps exist on the character of seamount spatial heterogeneity. Spatial pattern metrics, commonly used in landscape ecology, offer opportunities to quantify habitat heterogeneity and generate insights into spatial characteristics relevant for representational ecosystem-based management. This chapter used a top-down classification to identify geomorphological classes at five Southwest Indian Ridge seamounts that varied in topography, and proposed spatial pattern metrics from landscape ecology to quantify and compare seascape heterogeneity within and between seamounts.

Whilst part of the same regional geological feature (mid-ocean ridge system), seamounts differed in seascape composition and configuration. Five geomorphological classes occurred across sites: summit, slope, south-east facing and north-west facing flanks and ridges. Apart from flanks, all classes differed in spatial characteristics, and metrics most useful to distinguish between classes (considered 'patch types') were related to patch shape and patch clustering, with ridges most dissimilar to other classes. Across seamount seascapes, the spatial distribution of patches (occurrences of each geomorphological class) differed in number, shape, patch aggregation and intermixing. These variables allowed seamounts to be scored on a gradient from low spatial heterogeneity (large, aggregated and isolated patches) to high spatial heterogeneity (small, disaggregated and highly interspersed patches).

Although seamounts have been conceptualised as similar features, this study revealed quantitative differences in seascape spatial heterogeneity between seamounts. As variations in relative proportion and spatial relationships of patches within seamounts may influence ecological functioning, the proposed quantitative approach will help generate insights into within-seamount characteristics and seamount types relevant for representational ecosystem-based management. Further research into biodiversity associations with seascape composition and configuration at relevant spatial scales will help improve interpretation of the ecological relevance of different seascape metrics.

2.1 Introduction

Seamounts, typically defined as undersea mountains rising steeply from the seafloor, are some of the most prominent and widespread features of seabed topography globally (Yesson et al., 2011). They host distinct and vulnerable benthic communities forming complex biogenic habitats, and support mobile megafauna such as commercially important fish, marine mammals, and sea birds (Clark et al., 2019; Letessier et al., 2019; Morato et al., 2010; Rowden et al., 2010). The high environmental heterogeneity in seamount environments, such as variation in substrate type, topographic relief, and hydrodynamic exposure (McArthur et al., 2010) contribute to the ecological importance of seamounts and the high variability in faunal assemblages and distributions observed among and within individual seamounts (Rogers, 2018). Seamounts typically have a higher proportion of hard substrate types than the surrounding seabed environment (Stocks & Hart, 2007), which provides attachment opportunities for sessile seamount benthos (Rogers, 2018; Rogers et al., 2007). These communities in turn form complex biogenic habitats on summits and flanks that provide food and shelter for a wide range of smaller mobile species such as molluscs, crustaceans, echinoderms and demersal fish (Rogers, 1994; Samadi et al., 2007). By rising from the surrounding seafloor, seamount topography also modifies the local hydrodynamic regime. This may create distinct flow features, such as internal tides, mesoscale eddies and Taylor columns (Roberts et al., 2020), that affect geochemical cycling and nutrient mixing by nutrient upwelling or trapping of small organisms. These are hypothesised to attract larger marine predators

and fish aggregations forming spawning or nursery habitats (Pitcher et al., 2007; Rogers, 1994). Topography also influences the exposure of sessile suspension-feeding organisms to nutrient-rich (Du Preez et al., 2016; Rogers, 2018; Samadi et al., 2007). Seamounts may further offer biological refugia (Rowden et al., 2010) and seamount clusters may function as stepping stones for biological dispersal and connectivity (Miller & Gunasekera, 2017).

Although seabed heterogeneity has long been recognised as a main driver of biodiversity in deep-sea environments (McClain & Barry, 2010; Thistle, 1983), its spatial geometry is rarely quantified. Quantitative knowledge of environmental heterogeneity is key for a better understanding of seamount ecology, and could lead to insights into the potential ecological implications of spatial structuring of habitats that host and support seamount biodiversity (Clark et al., 2012; Swanborn et al., 2022). Addressing knowledge gaps around the character and consequences of benthic seascape heterogeneity is a priority because extensive physical disturbances change the spatial structure of seamount seascapes (Watling & Auster, 2017). Notably, trawling directly modifies benthic habitat mosaics with long-lasting effects due to low benthic recolonisation rates (Huvenne et al., 2016; Williams et al., 2020). A pattern-oriented approach facilitates comparisons between the structure of different seamounts, which can provide critical knowledge to classify seamount ecosystems for representational protection of their characteristics through MPA networks (Clark et al., 2011a).

Advances in mapping technologies and analysis techniques provide broad-scale maps from which environmental surrogates for biological communities in the deep sea can be derived (Howell et al., 2020). Measures of geomorphological structure (Wilson et al., 2007) and substrate types extracted from continuous bathymetry and backscatter acoustic maps are used as proxy for benthic communities' potential occurrence and distribution, and form input for benthic habitat maps (Brown et al., 2011). These segment and classify seascapes into areas of similar abiotic conditions that may be associated with a particular biological community. Land- and seascape ecologists have developed a wide range of analytical tools to quantify spatial heterogeneity from patch-mosaic representations as benthic habitat maps, focusing on the composition

(patch types and their relative amount) and configuration (the spatial arrangement and orientation of patches) of seascapes (Swanborn et al., 2022; Wedding et al., 2011). Variations in composition and configuration influence assemblage make-up, biodiversity patterns and organism movement, and ultimately ecological processes across the seascape such as structural and functional connectivity (Pittman et al., 2021).

The remote locations of most seamounts and the high cost of deep-sea exploration has resulted in only a small proportion of seamounts, most of which are located in the northern hemisphere, being sampled for scientific purposes (Kvile et al., 2014). This chapter focuses on five seamounts on the Southwest Indian Ridge (SWIR), which is one of the world's slowest spreading ridges (Sauter & Cannat, 2013). These seamounts are amongst the least scientifically studied globally (Demopoulos et al., 2003), but are located in a geographic zone at high risk from fishing (Clark et al., 2011a) and have been targeted by industrial fisheries for decades (Marsac et al., 2020; Rogers et al., 2017). Data on these seamounts remain sparse, but global predictive modelling studies have linked the SWIR to potential habitat for vulnerable communities (Yesson et al., 2012) and indicate high vulnerability to human impacts (Clark et al., 2010; Marsac et al., 2020). At present, little is known about the spatial patterns in terrain geomorphology (e.g., slope, topographic complexity) and patch-mosaic structure (i.e. seascape composition and configuration) of individual SWIR seamounts.

This study quantifies and compares spatial heterogeneity represented in geomorphological class maps from five SWIR seamounts varying in summit depths, shapes and sizes. The aims were to: 1) map and identify geomorphological classes on SWIR seamounts; 2) quantify and compare spatial environmental heterogeneity to test whether studied classes and seamounts differ in geomorphological structuring; and 3) evaluate which metrics were most useful to discriminate spatial heterogeneity in composition and configuration within and between seamounts.

2.2 Methods

Data used in this chapter were collected during RRS *James Cook* NERC cruise JC066 in November and December 2011 (Rogers & Taylor, 2012). Surveyed seamounts

(Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Seamount and Atlantis Bank) vary in shape, size and summit depth (Fig. 2.1, 2.2), and are located in different water masses. More extensive morphological descriptions can be found in Muller (2017), and more detailed maps of each individual seamount are included in Fig. A.1.1 to A.1.5 in Appendix A.

2.2.1 Study sites

Coral Seamount (41°28'S, 42°53'E) is located on a transverse ridge to the east of the Discovery II Fracture zone. It is roughly triangular with a summit located at 200 m depth and is elongated from north to south over approximately 18km. Different slope gradients and morphologies characterise the flanks of the seamount. Coral is the only surveyed site located in cooler waters south of the productive Agulhas Return Current and Subtropical Front and is accepted as an Ecologically and Biologically Significant Area (EBSA) under the Convention on Biological Diversity (CBD, 2015).

Melville Bank (38°28'S, 42°44'E) is located on the eastern side of the Indomed Fracture Zone, 45 km north of the SWIR axial valley, and stretches from east to west over approximately 13.5km. The shallower summit is characterised by ridges from north to south and east to west resulting from recent mass wasting events. The flanks show structures including embayments, chute structures and debris deposits.

Middle of What (MOW) Seamount (37°59'S, 50°24'E) is located 30km south of the mid-axial rift valley on a rim flank uplift. It is the only surveyed location not associated with a transform fault. MOW seamount is small in height and extent, stretching over 12km, and has a deeper summit (975m, Fig. 2.2) than other surveyed sites. The flanks show different morphological features, including terraces, cones and east-west faults.

Sapmer Seamount (36°5'S, 52°6'E) is located on the west flank of the Gallieni Fracture zone. The seamount is roughly triangular-shaped and extends 17km north to south along the fracture zone. The summit is truncated at approximately 250 m depth and features irregular, rough bathymetry (Fig. 2.2). The flanks exhibit different slope gradients and are characterised by slope failure processes. Sapmer seamount also exhibits flank rift zones in the form of volcanic ridges.

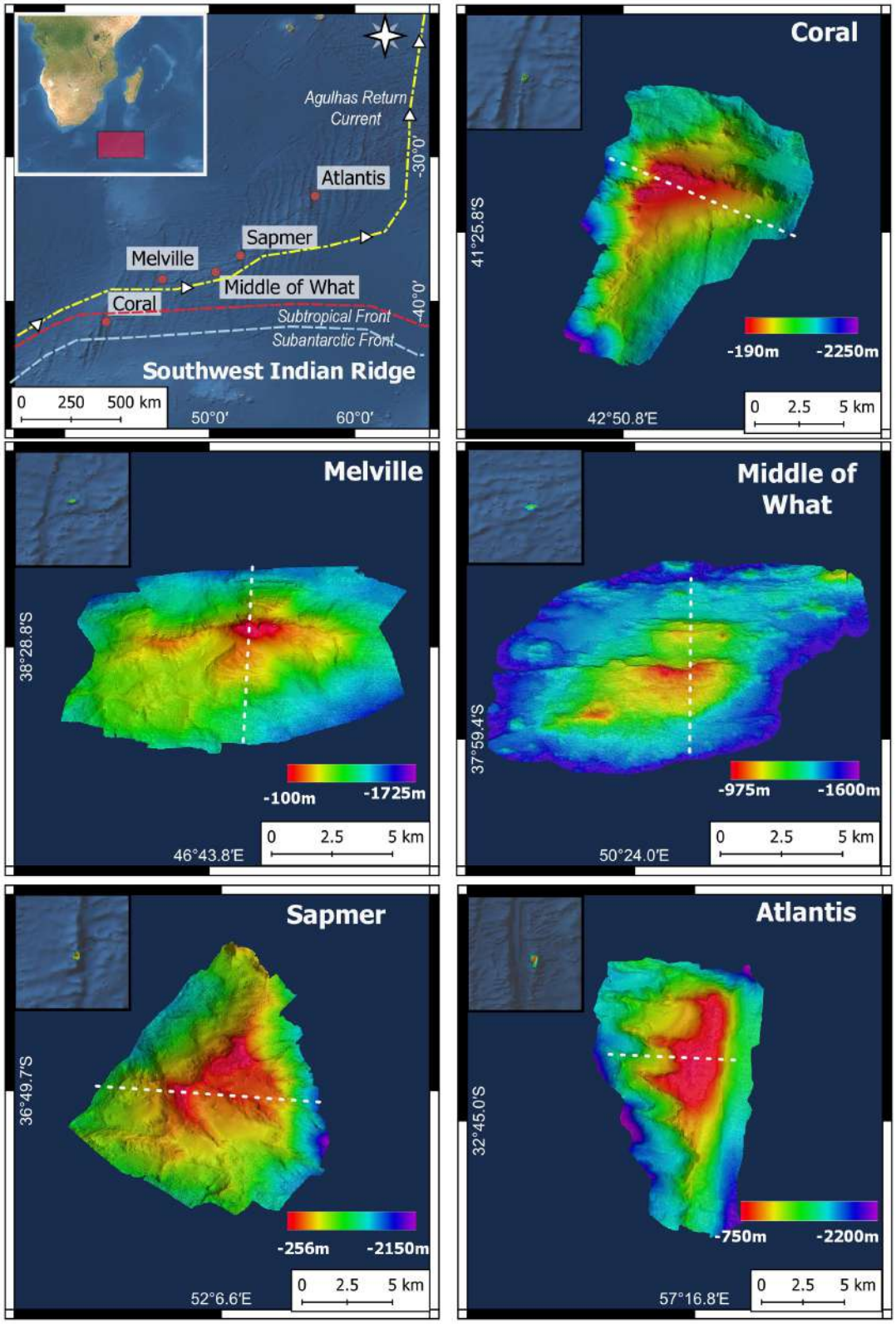


Figure 2.1: Surveyed seamounts on the Southwest Indian Ridge. Individual images show seamount topography, and insets show surrounding geological context (GEBCO). White dashed lines indicate locations of cross sections in Figure 2.2. Note differences in scale and depth ranges between seamounts.

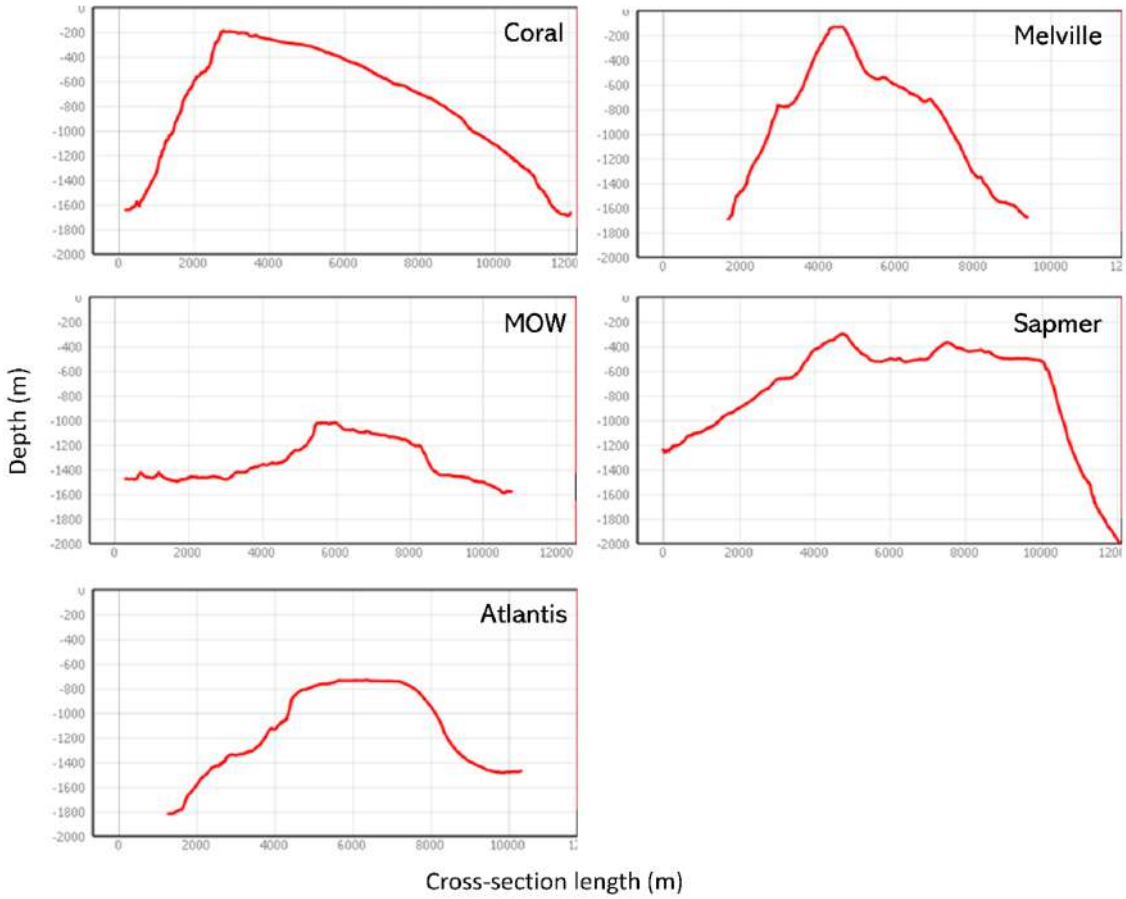


Figure 2.2: Profile plots of seamounts between 0 and 2000 m depth. Locations of cross sections are indicated as white dashed lines in Fig. 2.1. Profiles were taken in west-north-west to east-south-east direction at Coral, west to east direction at Sapmer and Atlantis, and in north to south direction at Melville and MOW. X values represent the length of the cross-section in m (12 km)

The morphology and origin of Atlantis Bank (32°45'S, 57°16'E) is covered in the literature and has been important in understanding the geology of ultraslow spreading ridges (Dick et al., 2019). It is an oceanic core complex created through fault action (Baines et al., 2003) and stretches north to south 14km along the Atlantis II Fracture Zone. The summit is flattened at a depth of 700 m (Fig. 2.2), resulting from historic wave erosion from when it was at or close to the sea surface. The western side features multiple embayments created through mass wasting events, forming rugged areas with steep slopes and cliffs. Atlantis is located in the Sub-Tropical Anticyclonic Gyre and has been designated a Benthic Protection Area (BPA) by the Southern Indian Ocean Deep-Sea Fisheries Association (Shotton, 2006) and, like Coral, an EBSA (CBD, 2015).

2.2.2 Data collection

Swath bathymetry and backscatter data were acquired during cruise JC066 using a hull-mounted Kongsberg-Simrad EM120 multibeam echo sounder, operated at a frequency of 12 kHz and used with the maximum 191 beams, giving 150° coverage (Muller, 2017). Any pings from beam angles greater than 120° were discounted to reduce errors. Adverse weather conditions, specifically rough sea states resulting in bubble entrainment, provided lower quality backscatter for Coral and Melville (Muller, 2017). Backscatter maps can be found in Fig. A.2.1 in Appendix A). Produced .all files incorporating navigation and sound velocity corrections were obtained from the British Oceanographic Data Centre (BODC) in September 2020, and further manual editing was conducted in Qimera 2.3.1 (swath bathymetry) and FMGeocoderToolbox (FMGT) 7.9.5 (backscatter) to remove erroneous soundings. Backscatter images for Coral and Melville were subsequently smoothed using a low-pass filter in QGIS 3.12 to reduce the strength of data artefacts. Data products were gridded to a resolution of 25m.

2.2.3 Analysis

The analysis consisted of three steps: 1) scale selection and terrain analysis; 2) classifying seamount seascapes in broad-scale geomorphological classes or patch types; and 3) quantifying seascape composition and configuration represented in benthic maps. Steps 1 and 2 followed an objective unsupervised classification technique (Ismail et al., 2015; Verfaillie et al., 2009). Statistical analyses were conducted in RStudio using R v3.6.3.

The quantification of terrain morphology was conducted at two spatial resolutions: the spatial resolution of the digital bathymetric model (25 m) and a broader resolution (275 m) determined using the Estimation Scale Parameter technique (Drăguţ et al., 2010). This multiscale approach detects the scale at which an abrupt rate of change occurs in local variance (ROC-LV) and considers this the appropriate resolution to resolve potentially important landscape features. LV was calculated as the average standard deviation within a 3 × 3 moving window over 25 m spatial scale increments on bathymetry data layers created through bilinear interpolation. A combined ROC-LV curve (Fig. A.3.1 in Appendix A) was produced by considering its average value across

scale levels to calculate the appropriate broad scale resolution across sites. A first break in the ROC-LV occurred at 275m and was therefore taken as the resolution to calculate broad-scale predictors. Multiple ecologically relevant variables measuring seamount geomorphology were quantified from bathymetry at the two focal spatial scales (25m and 275m) (Table 2.1). Considering the large depth differences between seamounts, individual seamount depth ranges were scaled before combined clustering to focus on within-seamount heterogeneity in geomorphological characteristics.

Table 2.1: Terrain metrics extracted from bathymetric data

Terrain variable	Description	Produced in:
Depth	Bathymetric surface representing depth	Qimera 2.3.1
Slope (Horn, 1981)	Rate of change of depth	R raster package
Eastness (Horn, 1981)	Direction of slope: orientation on east-west scale	R raster package, sin(aspect)
Northness (Horn, 1981)	Direction of slope: orientation on north-south scale	R raster package, cos(aspect)
Total curvature (Zevenbergen & Thorne, 1987)	Second derivative of seabed terrain, describes relative position of features	R spatialEco package, 3x3 neighbourhood
Topographic position index (TPI) (De Reu et al., 2013)	Elevation of cells (positive or negative) compared to neighbouring cells using mean deviations	R spatialEco package, 3x3 neighbourhood
Terrain ruggedness index (TRI) (Riley et al., 1999)	Local variation in seabed terrain around a central pixel	R spatialEco package, 3x3 neighbourhood
Vector ruggedness measure (VRM) (Sappington et al., 2007)	Measure of ruggedness in three dimensions	R spatialEco package, 3x3 neighbourhood
Slope of slope	Rate of change of slope; measure of terrain complexity	R raster package
Backscatter	Measure of reflectivity of seabed, corresponding to substrate type	FMGT 7.9.5

Unsupervised classification

The full dataset consisted of the values of terrain derivatives, backscatter and depth at each pixel across sites, standardised to zero-mean and unit-variance to have equal

weight in the analysis. The unsupervised classification consisted of two steps: Principal Component Analysis (PCA) and K-means clustering.

PCA was used to reduce data dimensionality and remove collinearity of input variables (Jollife & Cadima, 2016), which is frequently the case with derivatives extracted from the same bathymetric surface. The PCA procedures compute a set of Principal Components (PCs), linearly independent variables, from the spatial data layers representing terrain structure. The eigenvalues of the PCs can be used to determine which principal components to retain. The Kaiser Harris criterion prioritised principal components (PCs) for subsequent analysis, retaining PCs with eigenvalues larger than 1.

The PCs were subjected to K-means clustering (Hartigan & Wong, 1979). K-means defines homogeneous clusters that minimise the Euclidian distance in the multidimensional PC space between sample points and their allocated cluster centre. It starts with a random allocation of class centres using multiple starting points, followed by iterations to find a convergent solution where subsequent shifts in class centres stay below a pre-set threshold. The optimum number of clusters was determined using elbow plots. These visualise the intra-cluster variation (total within-cluster sum of squares), which clustering solutions aim to minimise, as a function of the number of clusters. The location of a bend in the plot, corresponding to a change in slope gradient, was chosen as appropriate number of clusters. It indicates where adding additional clusters does not significantly improve the total within-cluster sum of squares, reducing the risk of overfitting. The bend in the plot at 5 clusters (Fig. A.4.1 in Appendix A), corresponding to a change in slope gradient, was chosen as the appropriate number of clusters.

The K-means clustering algorithm, ran using 5 clusters and 500 random starting configurations, assigned each pixel of the input data a cluster membership. This final cluster solution was used to produce geomorphological class maps showing each pixel's cluster membership at each site. The character of obtained geomorphological clusters, was identified by creating boxplots showing each cluster's range of environmental characteristics.

Quantifying and comparing seascape structure

For the purpose of analysis, identified geomorphological classes were considered 'patch types' that occurred in multiple patches. To assess variability in seascape composition (amount and variety of patches) and configuration (spatial geometry of patches), spatial pattern metrics were extracted from the produced maps using Fragstats v4.12 (McGarigal et al., 2012) (Table 2.2). Metrics were chosen to quantify aspects of the seascape that are thought to be ecologically relevant (Wedding et al., 2011) (Table 2.2).

Spatial pattern metrics can be calculated at multiple levels of analysis: the individual patch, the class or patch type, and the overall seascape. This study selected metrics at the class and seascape level. Class-level metrics allow for comparing the composition and configuration of each identified geomorphological class across sites, whereas seascape-level metrics were applied to each seamount's entire benthic map to allow comparisons among locations. Class-level metrics were calculated using the mean value (sum of patch type metric values divided by the total number of patches), providing a patch-centric perspective. Seascape-level metrics were based on the area-weighted mean patch characteristics that correct for the relative size of patches (McGarigal & Marks, 1995).

Table 2.2: Patch-based spatial pattern metrics extracted from benthic maps

	Metric type	Fragstats metric	Description
Composition	*Area metrics*: basic metrics describing area composed by patches	Percentage of landscape (PLAND)	Relative proportion of each patch
		Mean patch size (AREA)	Average size of individual patches
	Diversity metrics: describe the compositional makeup of the landscape	Shannon diversity (SHDI)	Composite measure incorporating richness (number of different patch types) and evenness. Larger values indicate greater number of patch types and/or evenness.
		Shannon evenness (SHEI)	Describes the distribution of area among patch types. Equals one when area is distributed evenly.
Configuration: spatial arrangement of patches	*Shape metrics*: unitless metrics describing geometric complexity of patch shapes	Shape index (SHAPE) (Patton, 1975)	Perimeter area ratio corrected for patch size, where patch shape is compared to a square of the same size. Increases as patch shape becomes more complex.
		Gyration (GYRATE)	Mean extent of patch. Higher indicates more elongated patch.
		Contiguity index (CONTIG) (LaGro, 1991)	Patch shape is assessed based on the spatial connectedness of patches. The CI increases with larger contiguous path shapes.
	Isolation metrics: describe the degree of spatial isolation of patches	Euclidean Nearest Neighbour Distance (ENN)	Shortest straight-line distance between the centre of a focal patch and the centre of nearest neighbour of the same class
		ENN coefficient of variation (ENNCV)	Patch dispersion: the larger, the more irregular distribution of patches
	Subdivision metrics: describe the degree to which landscape is broken up in different patches	Number of patches (NP)	Number of different patches in landscape: the higher, the more fragmented
		Patch density (PD)	Number of patches per unit of area
		Splitting index (SPLIT) (Jaeger, 2000)	Degree of subdivision; increases as the landscape is increasingly subdivided into smaller patches.
	Aggregation and interspersion metrics: describe the spatial distribution and intermixing of patch types	Contagion index (CONTAG) (Li & Reynolds, 1993)	Measures the degree to which patch types are aggregated and mixed. The higher, the more aggregated the landscape is - i.e. few large contiguous patches – whereas lower values indicate higher interspersion and disaggregation

	Clumpiness index (CLUMPY) (class only metric)	Dispersion index depicting the deviation from a random distribution. (0). Small values (-1) indicate maximal disaggregation whereas higher values (1) indicate greater clumping.
	(normalised) Landscape shape index (LSI) (Patton, 1975)	Measure of total edge to area adjusted for landscape size. It can be interpreted as aggregation metric; the larger its value, the larger internal edge and disaggregation is, whereas smaller values indicate a compact landscape. The normalised LSI is scaled between 0 and 1.
	Interspersion and juxtaposition index (IJI)(McGarigal & Marks, 1995)	Interspersion index that measures the degree to which patch types are intermixed. The higher, the more evenly interspersed patches are in a mixture of patch types.

One-way Analysis of Variance (ANOVA) with pair-wise comparisons were used to assess whether class-level characteristics differed significantly ($p<0.05$) between geomorphological classes. Before conducting ANOVA, assumptions of normality and homogeneity of variance were checked using the Shapiro-Wilk test and Levene's test. Data were transformed using the Box-Cox family of transformations if assumptions were violated. At a seascape level, metrics with the largest variability were used to assess spatial heterogeneity between seamounts.

2.3 Results

2.3.1 Geomorphological class characteristics

The PCA procedure revealed nine significant (eigenvalue > 1) principal components that explained 90% of the total variance in predictor data (Table A.5.1 in Appendix A). Topographic ruggedness and slope contributed strongly to PC1, whereas PC2 consisted of depth, broad-scale curvature, and topographic position index (Table A.5.2 in Appendix A).

Benthic maps (Fig. 2.3) showed the distributions of five geomorphological classes (patch types) obtained through clustering the principal components. Maps were used in conjunction with boxplots (Fig. 2.4) and detailed bathymetry maps (Appendix A.1) to determine the character of identified geomorphological classes (Table 2.3). These were mainly distinguished by variations in slope, complexity, depth, and orientation. Class 1 consisted of shallower areas associated with the summit of seamounts. The terrain was flat and of low structural complexity, with local relief at individual seamounts. Class 2 was highly sloping (>20°), with elevated terrain complexity. Class 3 and 4 were both gently sloping flanks (5°-20°) and distinguished by orientation (class 3: south/south-east/east, class 4: north/north-west/west). At MOW and Melville, this included far-field terrain off the main seamount structure. Class 5 consists of highly structurally complex and sloping terrain, linked to local highs such as crests, ridges and scarps found on the tops of the seamounts and the edges of mass wasting features.

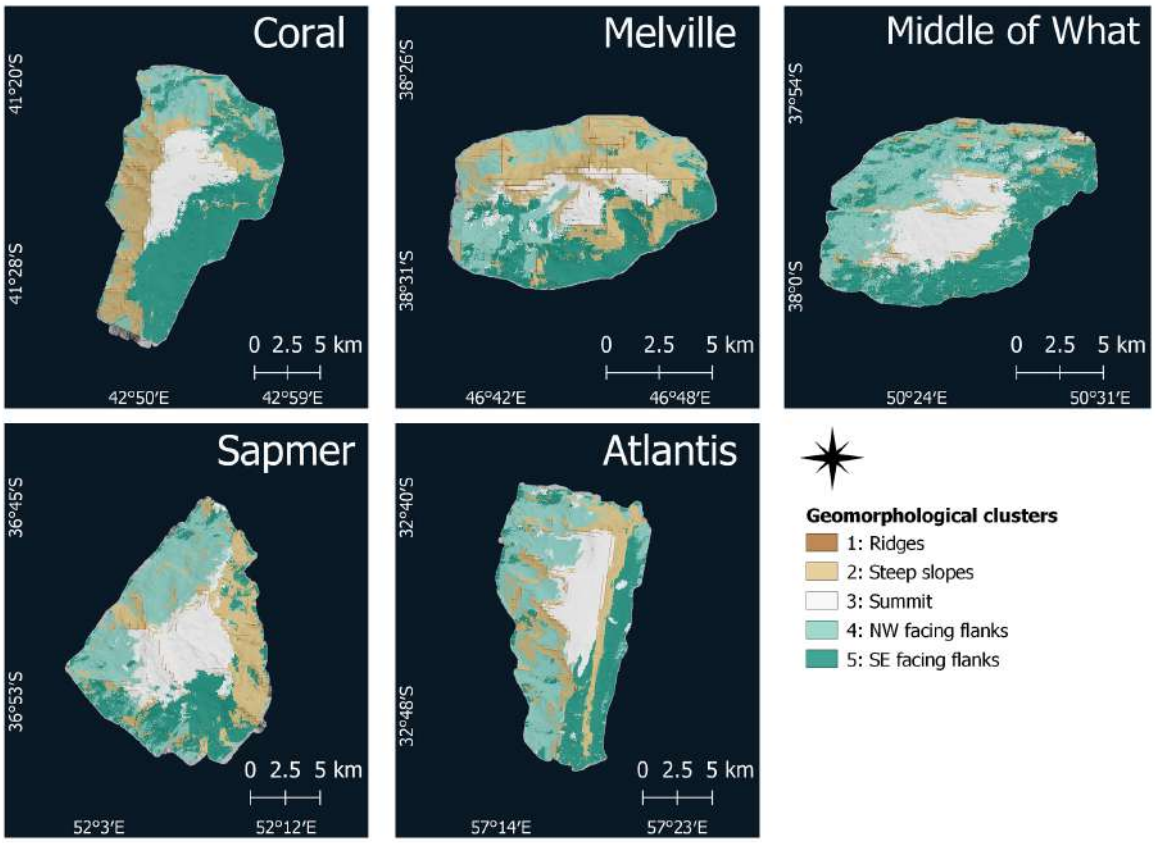


Figure 2.3: Distribution of identified geomorphological classes at each surveyed seamount

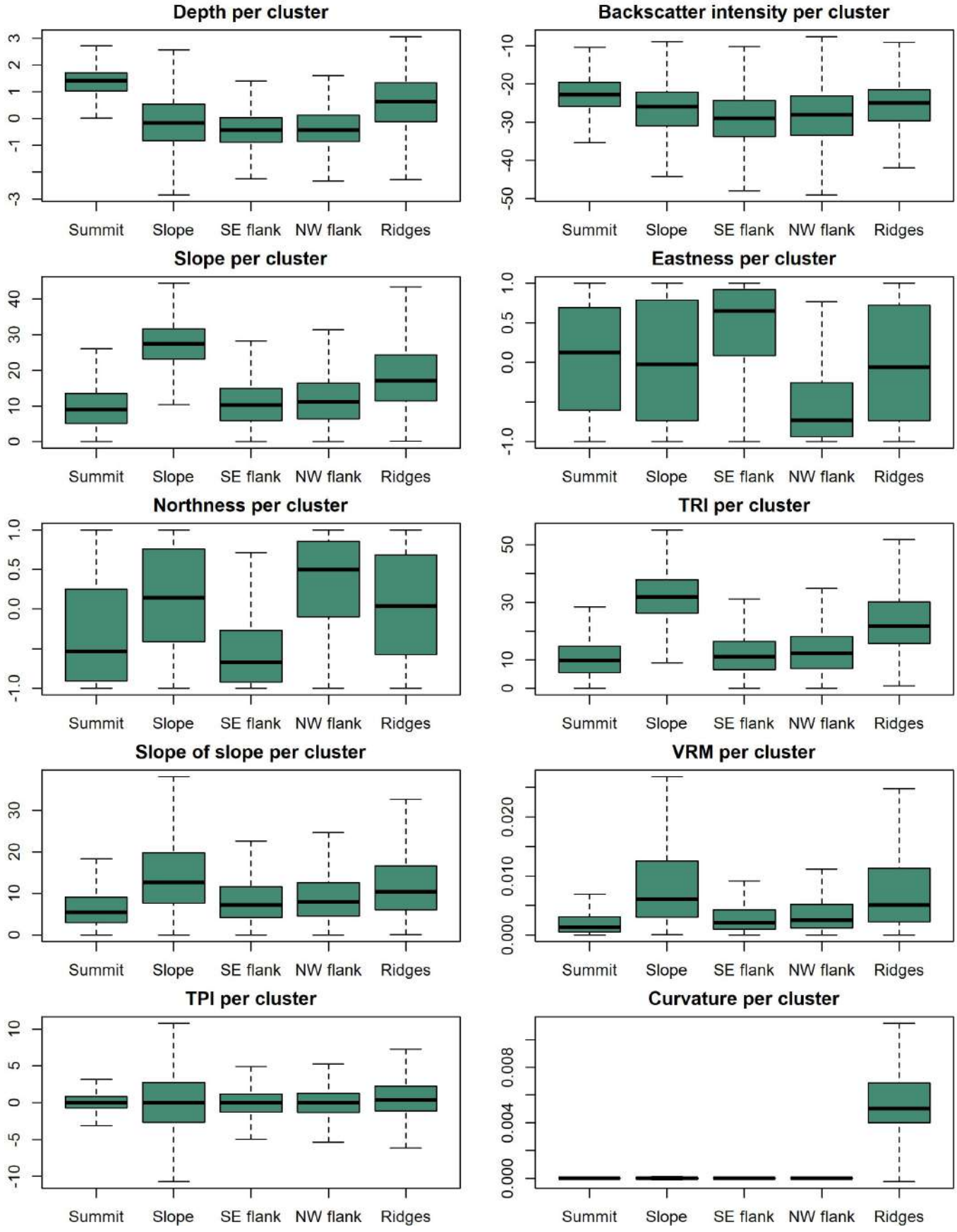


Figure 2.4: Boxplots identifying characteristics of each geomorphological class

Table 2.3: Summary table of geomorphological class characteristics and notable geomorphic features per site

	Description	Coral	Melville	MOW	Sapmer	Atlantis
Summit	Summit of seamount, lower relief	Summit at 190 m depth, relatively flat, featuring summit cones	Summit at 100 m depth; small, truncated plateau	Summit at 977 m depth, domed morphology and dipping to the north. North and south sections separated by a linear fault	Summit at 250 m depth, dipping to the south-east. Features local relief including domed areas and carbonate wave cut platforms	Wave cut platform at 750 m depth; high backscatter related to carbonate substrate
Slope	Highly sloping (>20°) flank	Located on west flank facing the fracture zone, featuring gullies and channels.	Steep chutes located around seamount summit associated with slope failures	Linked to fault scarps, smaller in extent than at flanks of seamounts	Located on east flank facing the fracture zone, with steep chute structures and small volume slope failures	Located around summit, associated with large transform parallel fault scarp (E) and steep chute structures (W)
SE flank	Southeast facing gently sloping (<20°) flank	SE flank with 5°-10° slope gradient and smooth surface, with linear faults cutting through	Flank areas with lower steepness and debris flow deposits from SE and SW slope failures (low backscatter)	Relatively flat (<10°), with SE facing lava terraces and volcanic cones (high backscatter) and areas of sediment accumulation (low backscatter).	Modified by slope failure processes, with arcuate headscar and broad embayment	Areas of lower steepness facing the fracture zone, lower backscatter indicating soft sediment
NW flank	Northwest facing, gently sloping flank (<20°)	Northern flank with lower steepness, features a broad ridge with lava terrace	Flank areas with lower steepness and debris flow deposits from SW, NW and NE slope failures (low backscatter)	Relatively flat (<5°), but dissected by faults and debris deposits (low backscatter) from fault scarp failures	Smoother morphology, and soft sediment (low backscatter), likely volcanic deposit	Western flank with four embayments as a result of slope failure processes, low and speckled backscatter associated with debris flows
Ridge	Highly structurally complex ridges	Structurally complex narrow ridges linked to flow structures on westward facing slope and adjacent to summit	Complex ridges and head scarps, associated with the summit and extending in the four cardinal directions	Raised areas of discontinuous topography, associated with volcanic cones	Volcanic ridges extending from summit and wave-cut platform on the summit	Complex ridges extending from the summit and located along major slope failures

2.3.2 Structural comparison between sites

To test whether studied patch types and seamounts differ in geomorphological structuring, class and seascape level metrics were applied.

Class-level

Class level metrics (Fig. 2.5, Table A.6.1 in Appendix A) quantified the spatial characteristics of identified geomorphological classes at each site, and ANOVA showed whether patch characteristics differed significantly between classes (Table A.7.1 in Appendix A).

Class 1. Class 1 (summits) had larger proportional abundances, patch area and gyration at Atlantis, Sapmer and MOW (Fig. 2.5a, b) and occurred in contiguous and simple shapes (Fig. 2.5d and e). The summits significantly differed from flanks and slopes in high aggregation and interspersion, and limited subdivision (Fig. 2.5h, j, k, Table A.7.1). Summit terrain at Melville was however disaggregated (Fig. 2.5h, i), deviating from this pattern.

Class 2. The relative abundance, mean size and extent of slope terrain differed across sites (Fig. 2.5a, b, c), with the largest proportional abundance at Melville and a limited area and extent at MOW. It significantly differed from other class types in a higher degree of contiguity and dispersion (Fig. 2.5e, g, Table A.7.1). Subdivision, aggregation and interspersion indices also showed reduced clumping and interspersion (Fig. 2.5h, i, j) at MOW.

Class 3. South-east facing flanks formed over 20% of seamount terrain at all sites apart from Sapmer (Fig. 5A) with largest patch size and extent at Coral and Atlantis (Fig. 2.5b, c). Aggregation and subdivision indices indicated an aggregated occurrence pattern with high clumping (Fig. 2.5h, i) and low splitting, but with reduced interspersion (Fig 2.5j).

Class 4. Composition and configuration of north-west facing flanks was not significantly different from south-east facing flanks (Table A.7.1). The relative abundance, mean size and extent of class 4 were variable per site with largest proportional abundance and patch area at Atlantis (Fig. 2.5a, b). Like class 3, distribution indices showed an aggregated occurrence pattern with least intermixing.

Class 5. Highly complex ridges of class 5 were significantly different from all other geomorphological classes in both composition and configuration (Table A.7.1). It occupied a smaller percentage of landscape with a small patch size and extent (Fig. 2.5a, b, c). Patches had more complex shapes (Fig.2.5d) and occurred in multiple small, disaggregated patches (Fig. 2.5h, i) that were spatially isolated and more dispersed (Fig. 2.5f, l) across sites than other geomorphological classes.

Seascape-level

Landscape-level metrics (Fig. 2.6, Table A.6.2 in Appendix A) compared overall seascape structure at each seamount. Composition-wise, sites differed in area (Fig. 2.6c, d), but not diversity metrics (Fig 2.6a, b). Configuration-wise, sites differed in seascape shape (Fig. 2.6e, f), subdivision (Fig 2.6i, j, k) and seascape aggregation (Fig 2.6l, m, n. Seascape metrics were used to rank the seamounts from lowest spatial complexity (large, contiguous patches and aggregated landscapes) to highest spatial complexity (small and complex patches, subdivided and intermixed seascapes) (Fig. 2.7).

At Coral, composition and shape metrics showed that mean patch size (Fig. 2.6c) and contiguity (Fig. 2.6f) were large compared to other sites. Patch shapes were relatively simple (Fig. 2.6e), and aggregation metrics confirmed a clumped seascape structure (Fig. 2.6l) with low patch density (Fig. 2.6j).

At Atlantis, patches exhibited relatively large spatial extent (Fig. 2.6d) and shape metrics suggest uniform patch characteristics. Subdivision metrics (Fig. 2.6j, k) indicate reduced seascape subdivision whilst aggregation and interspersion indices (Fig. 2.6l) suggest clumping. Middle of What has smaller patch sizes (Fig. 2.6c), but with larger extent (Fig. 2.6d) and complex patch shapes (Fig. 2.6e, f). Subdivision and isolation metrics show many patches at high patch density (Fig. 2.6i, j) and close proximity (Fig. 2.6g). Aggregation indices confirmed high disaggregation (Fig. 2.6l, m and limited patch intermixing (Fig. 2.6n). This indicates a high number of small patches in an extensive matrix of another patch type.

Patches at Sapmer were larger (Fig. 2.6c) and relatively contiguous. Subdivision and isolation metrics show increased isolation (Fig. 2.6g) and landscape splitting (Fig.

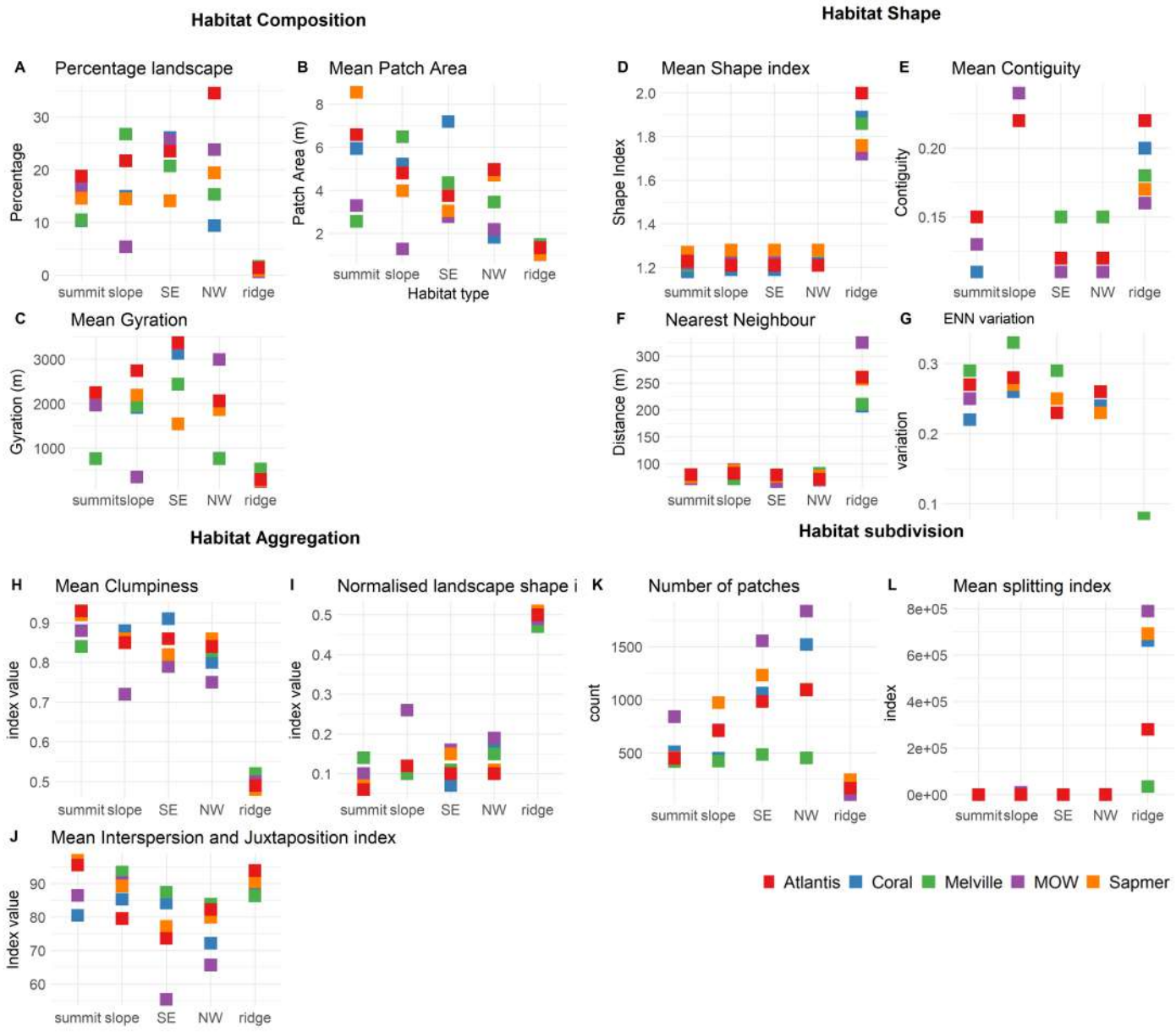


Figure 2.5: Class-level metric values for each geomorphological class per site, arranged by metrics of patch composition, shape, isolation, aggregation, subdivision and interspersion and juxtaposition

2.6k), which was matched by aggregation metrics confirming seascape disaggregation (Fig. 2.6m), reduced clumping (Fig. 2.6l) and, in contrast to Middle of What, intermixing of patch types (Fig. 2.6n).

Melville had the smallest mean patch size (Fig. 2.6c), and extent (Fig. 2.6d). Low contagion (Fig. 2.6l) and landscape shape (Fig. 2.6m) indicate limited clumping and high disaggregation, and dispersion and interspersion indices (Fig. 2.6n) show high intermixing of patch types.

2.4 Discussion

2.4.1 Geomorphological drivers of class types

The unsupervised classification identified similar geomorphological classes across seamounts, distinguished by variations in depth, slope, structural complexity and orientation. Depth is one of the primary determinants of marine biodiversity, including on seamounts, as it correlates with physical characteristics of the water column as temperature, oxygen, pressure, salinity, organic matter and light penetration. The classification established limited depth zonation within flanks and slopes. As a result of species replacement with depth these geomorphological classes likely host varying habitats and assemblages (Victorero et al., 2018), although they may be functionally similar by having comparable functional traits (de la Torriente et al., 2020). For example, steep slopes with rocky outcrops may host various cold-water coral assemblages that differ in species composition, but all function as filter feeders.

Slope, structural complexity and orientation distinguished flanks, summit and ridges. These variables may influence exposure to local hydrodynamic regime and the deposition of sediment and organic matter (Clark et al., 2010). Steep and structurally complex features experience reduced sedimentation, accelerate hydrodynamic flow, and can result in deep ocean mixing (White et al., 2007). Nutrient availability through such current amplification can positively promote the presence of coral habitat (Quattrini et al., 2012) and seamount associated fish (Leitner et al., 2021). Orientation has been used as proxy for hydrodynamic flow and exposure to the prevailing currents. However,

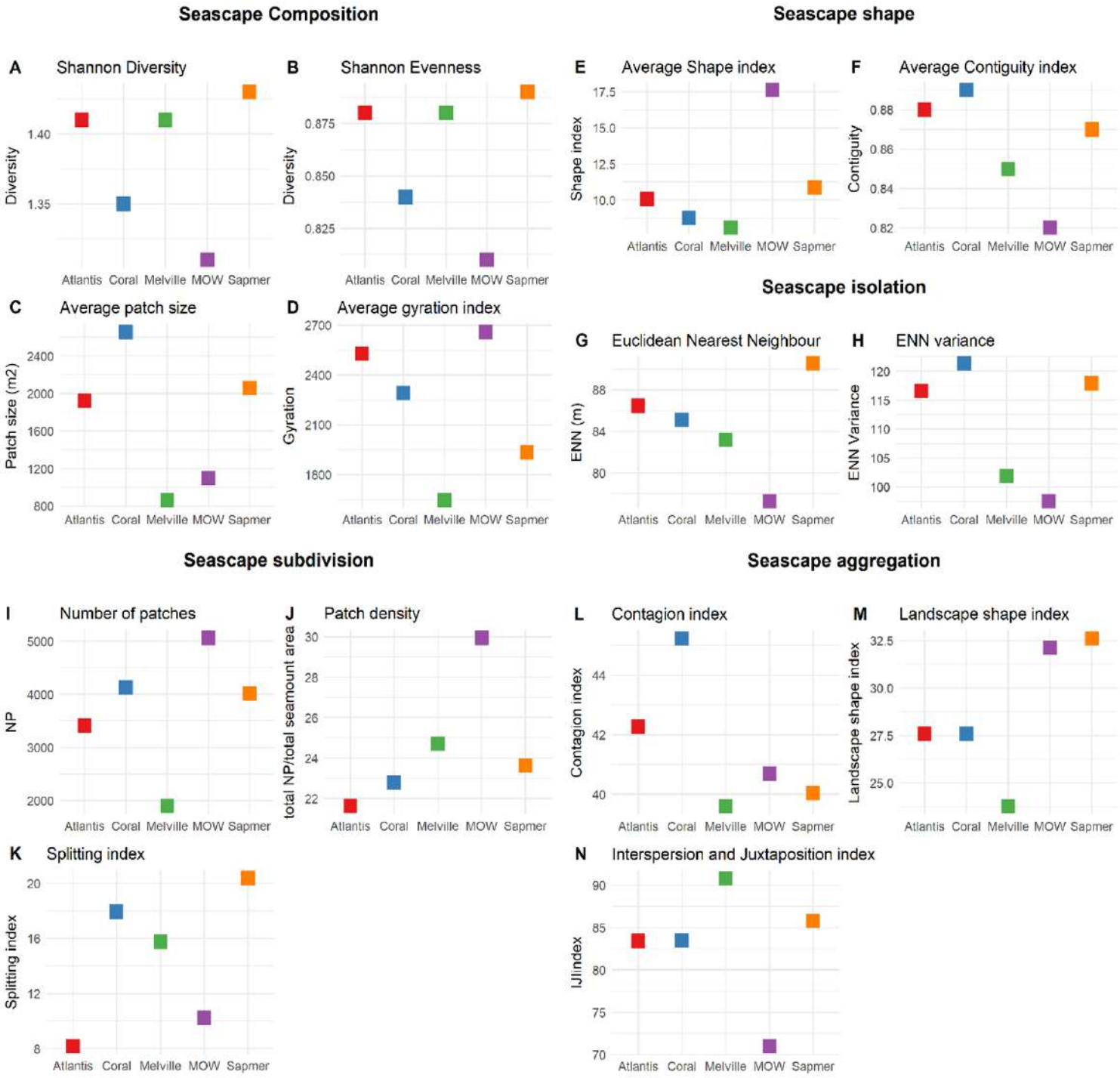


Figure 2.6: Seascape-level metrics per site, arranged by metrics of seascape composition, patch shape, isolation, subdivision and aggregation

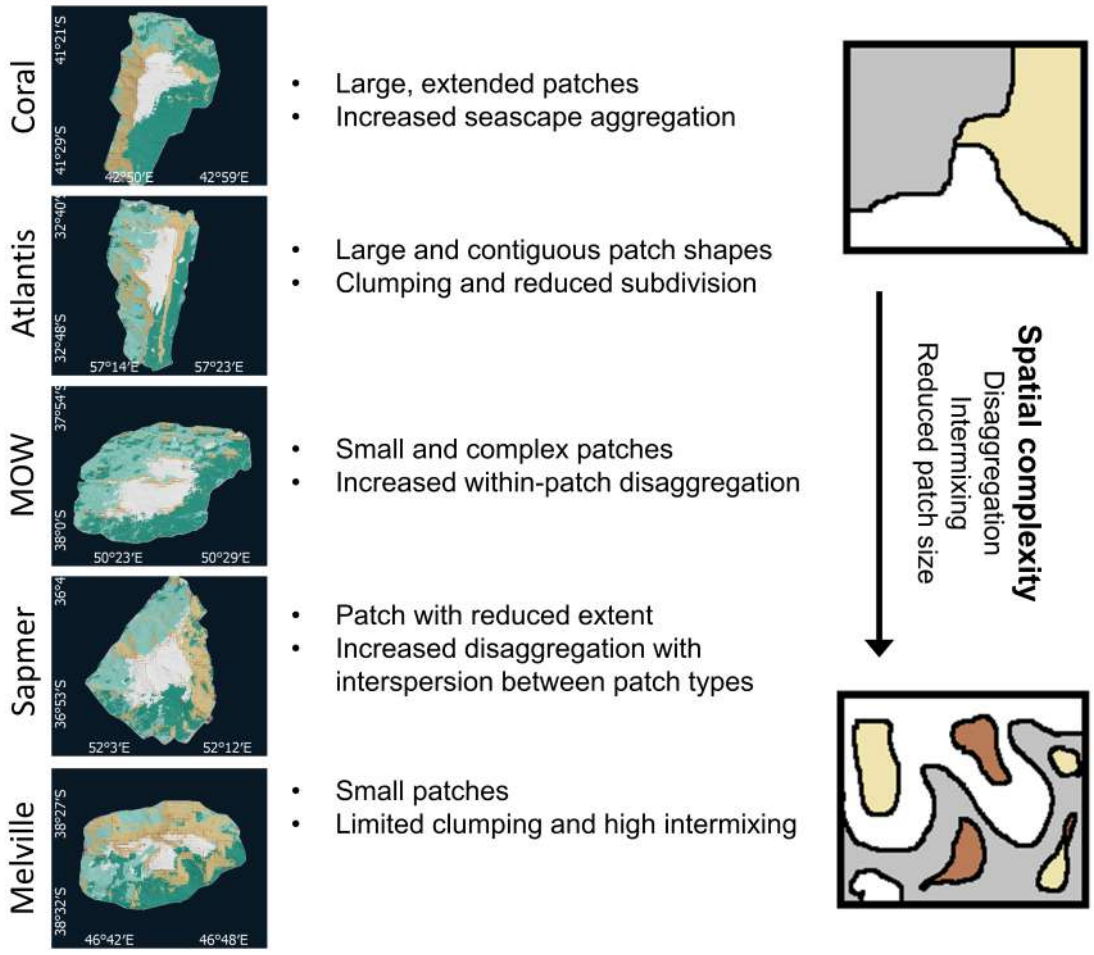


Figure 2.7: Sites scored along a gradient of increasing spatial complexity. Coral and Atlantis were spatially less complex with large, contiguous patches, whereas MOW, Sapmer and Melville were more spatially complex with a larger number of patches and varying degrees of aggregation and interspersion

prevailing currents differ across surveyed seamounts because of regional processes (Pollard & Read, 2017), and delineated flanks at seamounts might therefore not be directly comparable. Further research incorporating spatially explicit oceanographic parameters could help quantify environmental heterogeneity in current exposure.

2.4.2 Assessment of spatial heterogeneity

Class-level heterogeneity

Characteristics of identified geomorphological classes can function as predictors of benthic assemblage composition and distribution through biological associations with substrate types, structural complexity, hydrodynamic exposure and other environmental

parameters (Brown et al., 2011). Metrics showed class types also differed in composition and configuration, with possible implications for ecology.

Flat-topped seamount summits, class 1, are often associated with particular substrate types, relevant for sediment-associated epifauna and infauna (Rogers, 2018). The summits of Coral, Sapmer and Atlantis featured local relief as boulders, rocky outcrops, and carbonate pavement, providing attachment opportunities for sessile benthos (Rogers & Taylor, 2012)(Fig. 2.8a). This internal heterogeneity might also be ecologically relevant for certain mobile species, providing opportunities for different activities such as feeding or shelter (Fig. 2.8b). Hydrodynamic mixing of deeper nutrient-rich water upward over the summit (White et al., 2007) may be pronounced at sites with complex summit shapes such as Melville (Read & Pollard, 2017). Highly sloping flanks of class 2 are frequently associated with hard substrate for benthic settlement, and increased exposure to strong currents (Yesson et al., 2012). Video observations showed the steep western slope of Coral hosted a distinctive community of brachiopods, sponges, octocorals and black coral (Rogers & Taylor, 2012)(Fig. 2.8d). Class 2, steeply sloping terrain, was more spatially contiguous than other classes. Spatial contiguity might indicate structural connectivity important for habitat-specific species (Meynecke et al., 2008). Additionally, the interspersion between other class types might be relevant for seamount fish and marine mammals using a wider range of environments.

Classes 3 and 4 extended to greater depths. Backscatter data (Appendix A.2.1) and limited video observations (Rogers & Taylor, 2012) indicated these flanks were covered in soft sediment patches (Fig. 2.8e) important for benthic fauna (Durden et al., 2015) and mid- and deep water fish associated with soft substrate (Morato & Clark, 2007) (Fig. 2.8f). Flanks differed in their high spatial aggregation and large patch types, indicating extended core habitat availability but limited connection to other patch types. Combined with greater depth, these flanks are likely inhabited by specialised communities. Evidence of trawling and fishing-associated litter (Woodall et al., 2015) suggests that these large flank terrains with limited vertical relief to impede trawling (Clark et al., 2011b) are at risk of anthropogenic effects. Such disturbance can result in habitat fragmentation, impacting the highly aggregated character of these class types.

The ridges and crests that compose class 5 have high structural complexity and hard substrate, likely promoting exposure to flow. Evidence for such bathymetrically modified hydrodynamic features over ridges was observed at Coral, Melville and Sapmer (Read & Pollard, 2017). Observations supported diverse biogenic habitats at ridges, with dense communities of coral, large sponges, anemones, stylasterids, black corals, octocorals and brachiopods (Rogers & Taylor, 2012)(Fig. 2.8c) which may also benefit fish assemblages (Leitner et al., 2021; Quattrini et al., 2012). The small size and fragmentation of ridge terrains show that they are typically limited and dispersed across seamount seascapes, possibly providing hotspots of highly diverse and productive benthic habitat interspersed between other class types.

Seascape-level heterogeneity

Seamounts differed primarily in patch size and extent (composition) and in shape, aggregation and interspersion (configuration).

Composition -

The type and abundance of geomorphological classes influences biodiversity and ecosystem functioning (Zeppilli et al., 2016) and was measured by composition metrics. Although variable in proportional abundance, each seamount featured all five identified geomorphological classes resulting in limited variation in diversity metrics. However, area metrics varied across sites and showed Coral, Sapmer and Atlantis featured larger patch shapes. Under theoretical ecology, larger areas are predicted to host higher species richness (Turner & Gardner, 2015). Species-area relationships apply to deep-sea sessile benthic diversity across depth bands and substrate types (Foster et al., 2013), and are therefore likely applicable to seamounts too. Deep-sea mobile megafauna may be habitat specialists and predictably associated with geomorphological class features (Quattrini et al., 2012). The occurrence and abundance of some habitat-specific mobile megafauna may be linked to minimum area requirements and influenced by the gyration index (extent), which was particularly large for MOW, Atlantis and Coral. However, as minimum area requirements are unknown for many deep sea species environments knowledge gaps remain the transferability of such concepts.

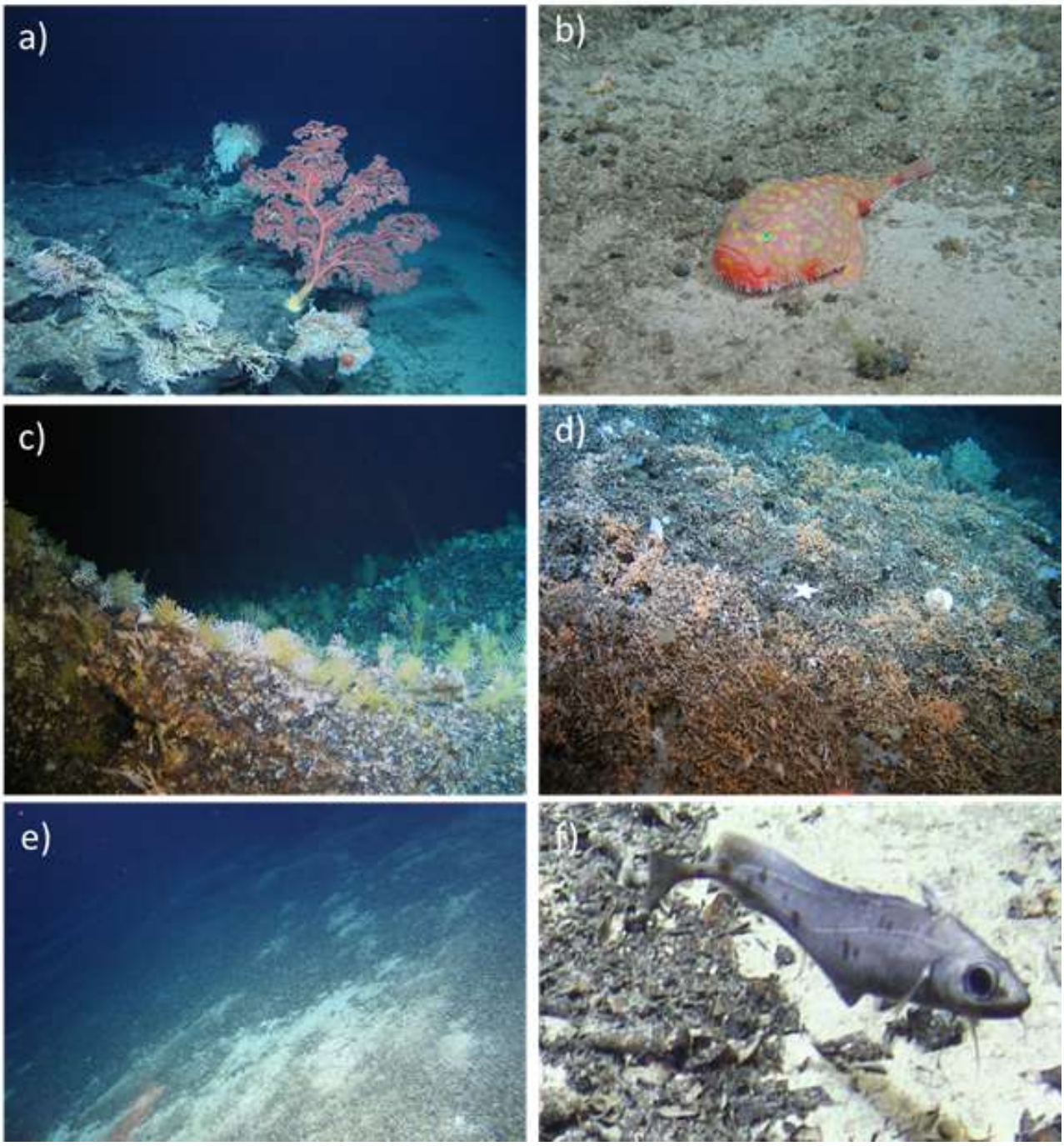


Figure 2.8: Selected ROV observations from different geomorphological classes. a) attachment opportunities on flat-topped summit at Atlantis, b) *Chaunax stigmaeus* resting on a sandy patch on the summit of Sapmer, c) Summit and ridge terrain at Melville covered in dense mesophotic coral gardens, d) steep slope at Coral covered in coral framework, e) SE flank at Melville featuring patches of soft sediment and f) cod species on deep northern flank at Coral

Configuration -

Patch shape: Patch metrics showed that seascapes differed in patch complexity. Complex patch shapes are thought to offer limited core area and increased edge, resulting in greater exposure to external environmental conditions (Ries et al., 2017). These edge effects alter the habitat quality of patch edges in different ways, depending on biological traits and the quality differences between adjacent patch types. Average patch shapes at Coral and Atlantis were less spatially complex, suggesting increased availability of core habitat, whereas MOW featured more complex patch shapes. Edge effects are little studied in deep-sea benthic environments, but appear relevant in the context of physical disturbances (Harris, 2012). Additionally, transitions between broad-scale benthic class types may be less discrete than on land (Lucieer & Lucieer, 2009).

Aggregation and interspersion: Seascapes differed in aggregation and interspersion characteristics with possible implications for structural connectivity across the seascape. Little is known about the influence of structural connectivity on benthic and demersal fauna associated with the deep seabed, especially as many species disperse larvae through the water column (Swanborn et al., 2022). Patch aggregation is likely important for mobile habitat-specific species with limited dispersal ranges as they facilitate movement between patches of the same type. Coral and Atlantis featured more aggregated seascape characteristics, suggesting increased habitat connectivity. Conversely, the diversity in morphological features at Middle of What resulted in higher patch disaggregation and isolation. This has been linked to reduced connectivity in terrestrial habitats, which may impact metapopulation and community dynamics of mobile species. The intermixing of patch types, such as seen at Melville and Sapmer, meanwhile, may be ecologically relevant for migratory species as large predatory fish and marine mammals that use multiple habitat types across regions and depths of the seamount (e.g. feeding and shelter) (Holland & Grubbs, 2007).

2.4.3 Importance and methodological considerations

Relevance approach

When prioritising seamounts for protected area establishment or incorporation in marine protected area networks, an important consideration is ensuring that representative physical and biological features are included (Clark et al., 2014, 2011a), also recognised in Aichi Biodiversity Target 11 (Rees et al., 2018). Previous biogeographic classifications of seamount environments based on representation have been conducted at broad scales and did not incorporate patterns of seabed structure (Clark et al., 2011a). This chapter showed that seamounts differ in the proportional abundance and spatial characteristics of geomorphological classes. As these variations are likely biologically meaningful, spatial metrics could be valuable additions to broad-scale physical variables as depth and oceanographic parameters to group seamounts with similar characteristics. Based on this limited study of SWIR seamounts, the degree of aggregation and interspersion and patch shape complexity appear important descriptors of spatial variation.

This chapter also showed that composition and configuration can differ within individual seamounts. Different geomorphological classes could benefit from being incorporated in the case of protection of a subset of a single seamount. For example, a zoning plan focused on protecting a seamount summit might fail to incorporate spatial representation, as ridges, flanks, and steep slopes can host different biological communities with different vulnerabilities to impacts (Bo et al., 2021) but also have different spatial characteristics.

Transferability technique

Here, a top-down classification based on terrain derivatives was used to identify geomorphological classes. However, proposed approach of quantifying environmental heterogeneity using spatial pattern metrics also extends to seabed and habitat maps produced using other methods (such as geomorphons, landform elements, see Jasiewicz & Stepinski (2013), or bottom-up classifications). Further mapping efforts incorporating other environmental data sources could help the representation of other sources of environmental heterogeneity. For example, oceanographic variables and different

water masses strongly contribute to heterogeneity, mediated by the height of the seamount, its shape, size and fine-scale topography, and the strength of the current regime (Rogers, 2018). Studied seamounts were located in different water masses (Coral close to the Subantarctic Front, Melville, Middle of What and Sapmer by the Subtropical and Agulhas Fronts, and Atlantis in the Sub-Tropical Anticyclonic Gyre). Therefore ecologically important oceanographic parameters such as temperature, current velocity, dissolved oxygen and salinity likely differ between seamounts. Dynamic models incorporating spatio-temporal changes in oceanography might further refine obtained insights within seamounts (Kavanaugh et al., 2016) as oceanographic conditions at the seabed were variable over tidal cycles (Read & Pollard, 2017).

Scale-dependency and ground-truthing

This study did not consider a specific phenomenon but instead focused on quantifying and comparing broad-scale features. Although generalities will emerge, resolving the ecological implications of heterogeneity in seascape characteristics requires consideration of thematic scale. What constitutes a suitable habitat depends on the life history traits, life style (i.e. benthic, infaunal, epifaunal) and mobility of the species or process under consideration (Levin, 1992). As species-environment associations were not explicitly quantified and incorporated to inform the classification, produced maps do not intend to predict the occurrence and distribution of biological communities. However, uncovered broad-scale geomorphological classes exhibit internal heterogeneity that may be ecologically relevant for associated species, including different habitat types. Hierarchical classification approaches using ecological validation could help reclassify broad-scale entities into finer-scale physical habitat types and test the accuracy of identified class types and their spatial characteristics for particular species (Hogg et al., 2018). Considerations of appropriate thematic scale for the phenomenon under consideration will also improve the relevance and interpretation of spatial pattern metrics (Pittman et al., 2021). Seamount-associated sessile and mobile benthos have different habitat requirements than mobile megafauna as fish or mammals due to mobility ranges and life history traits.

Metric interpretation

The chapter also highlighted some uncertainties in the transferability of interpretations of landscape ecology metrics to deep-sea environments. Transitions between patch types may be less discrete (edge effects), and organisms have different dispersal strategies (water column). Also, the interpretation of metrics for sessile benthic organisms is less clear cut. Therefore, further multiscale studies testing the ecological relevance of seascape composition and configuration on sessile and mobile seamount biota are recommended, for example, generating predictor variables for explaining distribution patterns. Such knowledge would help further the conceptual importance of spatial pattern metrics from landscape ecology in heterogeneous deep-sea environments at scales appropriate for the phenomenon under consideration.

2.5 Conclusion

Using a quantitative approach combining unsupervised mapping and spatial pattern metrics, this chapter found that 1) SWIR seamounts hosted five similar geomorphological classes (summit, slope, south-east facing and north-west facing flanks and ridges) despite varying morphology; 2) SWIR seamounts differed in spatial composition and configuration at class and seascape level; and 3) at class-level, metrics of contiguity, isolation and clumping differentiated patch types, whereas at seascape-level patch area, intermixing and disaggregation distinguished seamounts. Spatial pattern metrics proved useful for quantifying spatial environmental heterogeneity and are transferable to benthic maps produced with different methods, but further research will help improve the interpretability of results.

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Author contributions

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DS: conceptualization, methodology, formal analysis, writing – original draft, writing-review & editing. ADR: funding acquisition, field data collection, writing - review & editing. MT: field data collection, writing - review & editing. VH, SP, LW: supervision, writing - review & editing.

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3 Seamount seascape composition and configuration shape Southwest Indian Ridge fish assemblages

Abstract

Seamounts are commercially important fishing grounds, yet little is known about their physical characteristics as fish habitat. This information is crucial for informing conservation and ecosystem-based management.

This chapter examines the influence of multiscale seabed spatial heterogeneity on the assemblage characteristics of commercially important fish families at three Southwest Indian Ridge seamounts (Coral Seamount, Melville Bank and Atlantis Bank). Seascape heterogeneity was quantified from bathymetry and geomorphological class maps, and 15 focal fish families were identified from video data. Using a seascape ecology approach, fish-habitat associations were examined using spatial pattern metrics that measured continuous terrain morphology, seascape composition (the variety and relative abundance of patch types), and seascape configuration (the spatial arrangement of patch types). Broader seascape context was characterised by geographic location and water depth. Machine learning algorithms (multivariate regression trees and random forests) modelled fish-habitat associations and identified the most influential explanatory variables.

Fish assemblages and individual families were strongly dependent on geographic location and depth, and at finer scales (500 m buffers) seascape composition and configuration helped explain fish-habitat associations. A high abundance and diversity of commercially important demersal fish were associated with spatially continuous summit terrain and complex shaped ridge features. Metrics of seascape composition and configuration (such as patch size, shape and structural connectivity) had higher

predictive power than the terrain derivatives commonly used in developing proxies for predicting distributions of deep-water fish species and biodiversity.

These outcomes indicate that patch mosaic metrics, proven to be ecologically relevant on land and in shallow-water marine environments, are also relevant for identifying environmental predictors of fish distributions in remote deep-sea environments. This chapter also highlights strong context dependency and depth-specific associations that hinder attempts at this point to draw generalisations on fish-seascape linkages for seamounts.

3.1 Introduction

Seamounts are elevated topographic features (>100 m) above the surrounding seabed (Yesson et al., 2011). They are recognised as hotspots of benthic and pelagic diversity and support a high abundance of demersal and benthopelagic fishes compared to the surrounding environment (Serrao Santos & Morato, 2008). Fish aggregations around these elevated topographic features have also led to the establishment of deep-sea fisheries (Clark, 2009). These fisheries can have high catch-per-unit-effort ratios and large ecological impacts, exacerbated by the low growth and high mortality rates of many seamount-associated species (Pitcher et al., 2007). Despite the ecological and economic importance of seamount-associated fish, fish-habitat relationships around seamounts remain poorly understood, with only a fraction of total seamounts sampled (Kvile et al., 2014). Very few studies have measured multiscale heterogeneity in benthic seascape structure to examine its ecological relevance for mobile marine species. A better understanding of the linkages between seascape characteristics and fish assemblages may have significant implications for ecology, ecosystem-based fisheries management and biodiversity conservation (Leitner et al., 2021; Santos et al., 2021).

Environmental gradients and patchiness in abiotic and biotic conditions are characteristic of seamounts. Varying topography, substrate types, the overlying hydrodynamic regime and benthic cover create gradients and patchiness in a range of habitat types, influencing biological diversity at the seafloor (Goode et al., 2021; McClain & Schlacher, 2015). Heterogeneity can be represented and quantified in terms of patch mosaic composition (the variety and relative abundance of habitat types), spatial configuration

(the arrangement of patches), and terrain surface morphology (Pittman et al., 2021; Wedding et al., 2011). Quantitative seascape ecology studies of the effect of seascape composition, configuration and terrain structure have yielded important insights into the fish communities of shallow marine systems including, for example, the importance of the type, size and shape of habitat features (Boström et al., 2011), their spatial configuration (Meynecke et al., 2008), and the influence of spatial scale and context (Forman, 1995; Pittman et al., 2004).

Studies measuring deepwater fish-habitat associations, including at seamounts, have predominantly focused on depth and substrate characteristics, revealing that deep-water fishes use a range of habitat types over different scales (Auster et al., 2005; Quattrini et al., 2012). Fish may use biogenic features for shelter or food sources (Rogers et al., 2007), feeding aggregations are seen on larger features such as summits and crests (Leitner et al., 2021; Morato & Clark, 2007) and soft-sediment areas of low complexity can host significantly different assemblages compared to complex habitat types (Devine et al., 2020; Ross et al., 2015). The diversity of broad-scale habitat or patch types and their abundance (seascape composition) is therefore ecologically relevant for mobile species across depths (Anderson et al., 2009; Borland et al., 2021). Additionally, the spatial characteristics of the local and surrounding seabed environment (seascape configuration) appear to influence the distribution and abundance patterns of deep-water demersal fishes (Anderson et al., 2009).

Despite an increasing interest in studying the influence of habitat characteristics on deep-water fish (e.g. Leitner et al. 2021), key knowledge gaps remain on the importance of the spatial patterns of habitat patches, terrains and the surrounding seascape for seamount associated fish, as well as on the transferability of theoretical frameworks developed on land to the deep ocean (Swanborn et al., 2022b). Yet, similar questions, concepts and quantitative techniques for measuring heterogeneity in terrestrial landscapes and in shallow waters may provide insights into the importance of environmental heterogeneity for demersal fish associated with seamounts. Improved data quality and availability of in-situ biological survey data collected using remotely operated vehicles (ROVs), combined with high-resolution bathymetry and habitat

mapping provide unprecedented opportunities to explore the ecological relevance of benthic seascape patterns on biological assemblages (Swanborn et al., 2022b).

The Southwest Indian Ridge (SWIR) seamounts remain poorly studied, yet have been subject to intense deep-sea fishing activity over the past 40 years (Rogers et al., 2017; Woodall et al., 2015). Some seamount aggregating species such as orange roughy (*Hoplostethus atlanticus*), pelagic armourhead (Pentacerotidae), oreos (Oreosomatidae) and alfonsino (*Beryx sp.*) are highly valued by commercial fisheries, leading to intense exploitation (Clark, 2009; Clark et al., 2007; Rogers et al., 2017). Although SWIR seamounts are known aggregation spots for commercially important species, little is known about the physical habitat characteristics that support them (Rogers, 2013). Knowledge on the potential function of seascape spatial patterns as a proxy for predicting fish assemblages can inform management, for example, by identifying and characterising priority areas for conservation (Clark et al., 2012; Moore et al., 2016).

This chapter aims to identify commercially important demersal fish families at three SWIR seamounts and examine the ecological importance of seabed environmental heterogeneity at multiple spatial scales for these families by employing the theoretical framework of seascape ecology. To identify ecologically important seascape features, this chapter assesses 1) whether seamount assemblages differ between depth zones and seamounts; and whether and what metrics of seascape composition and configuration are key drivers of 2) assemblage characteristics (abundance, richness and diversity) and 3) individual fish families.

3.2 Methods

3.2.1 Study locations

Data used in this chapter were collected during the 2011 JC066 cruise aboard RRS James Cook (Rogers & Taylor, 2012). The considered seamounts, Coral Seamount (Fig. 3.1b), Melville Bank (Fig. 3.1c) and Atlantis Bank (Fig. 3.1d), are located along the ultra-slow spreading SWIR and characterised by varying morphologies and summit depths. They are positioned within different regional oceanographic conditions

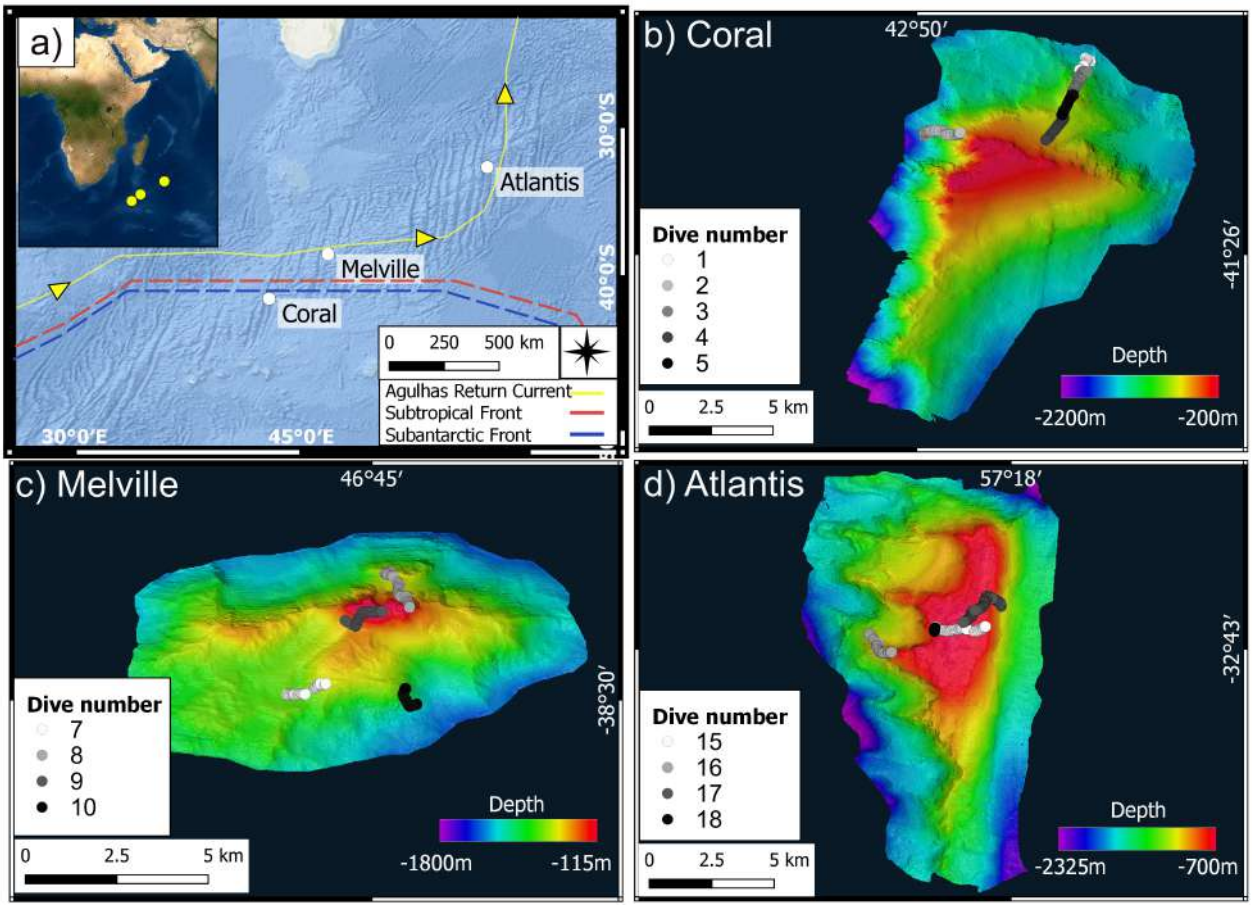


Figure 3.1: Surveyed SWIR seamounts described in Rogers and Taylor (2012. Panel a indicates the location of the three surveyed seamounts and dominant influences on local oceanography. Subsequent panels show multibeam bathymetry and location of ROV dives) at Coral (b), Melville (c) and Atlantis (d) (note different horizontal and vertical scales). Colour bars indicate seamount depth. Dives differed in depth range surveyed, dive time and distance covered. Dive 6 was a sample collection dive and therefore not included. Dive 11-14 were conducted at locations not considered in this study

created by the Agulhas Return Current, the Sub-Tropical Front and the Sub-Antarctic Front (Fig. 3.1a), which influence the biodiversity these seamounts host (Pollard & Read, 2017; Rogers et al., 2017).

3.2.2 ROV surveys

To survey demersal fish populations, upslope video transects were conducted with the ROV Kiel 6000 (Fig. 3.1). The ROV, where possible, was run at 1m above the seabed at approximately 0.2kts and carried a CTD for in-situ oceanographic measurements. While the sampled depth ranges overlap across the three features, as a result of weather

conditions and seamount morphology, sampling effort and average depth surveyed differed per site (Table 3.1). Dives at Melville Bank were conducted at the shallowest depths, Coral Seamount contained the majority of dives in the bathyal zone (> 1000 m) and Atlantis Bank contained predominantly dives in the twilight zone (200-1000 m).

Table 3.1: Characteristics of conducted ROV dives (Rogers and Taylor, 2012). Dives were semi-randomly selected to cover different aspects of each seamount and differed in depth range surveyed, dive time and distance covered.

Site	ROV Dive no.	Date	Depth range (m)	Dive time (min)	Distance (m)
Coral Seamount	1	12/11/2011	1400-1090	506	1533
	2	13/11/2011	1493-622	507	3518
	3	14/11/2011	1065-681	597	1870
	4	16/11/2011	745-510	270	2305
	5	20/11/2011	731-738	316	1025
Melville Bank	7	23/11/2011	900-671	442	1827
	8	24/11/2011	675-150	505	1946
	9	25/11/2011	380-125	414	1638
	10	26/11/2011	1295-970	334	972
Atlantis Bank	15	09/12/2011	720-748	640	2639
	16	10/12/2011	1100-825	385	1428
	17	13/12/2011	1000-720	519	3353
	18	14/12/2011	730-740	98	130
Total				**6649**	**29672**

3.2.3 Biological data

Continuous annotation of underwater video data collected by the ROV was conducted with QuickTime Viewer (Apple Inc.), where a screenshot was taken for every fish sighting during the dive (Malpas, 2017). Every sighting was then identified to the lowest taxonomic level possible (Malpas, 2017) using a combination of reference books (Gon & Heemstra, 1990; Whitehead, 1985) and the online database FishBase (Froese & Pauly, 2020). Substrate type (bedrock, boulders, cobbles, gravel, mud, coral rubble, cold-water coral reef, mesophotic coral reef) was also recorded from these screenshots according to the majority rule (>50% cover determines the substrate type). When

no substrate type was visible in the screenshot (e.g. as a result of camera orientation or bad visibility) substrate type was recorded as 'NA'. All sightings were linked to ROV track metadata using timestamps, which contained position (latitude, longitude, depth) and oceanographic data (temperature, salinity, pressure).

The continuous ROV dives were divided into separate transects to derive comparable sampling units. The appropriate transect length was determined by iteratively testing different transect lengths in steps of 25 m (the resolution of bathymetry) between 50 and 700 m, to find the length maximising both the number of transects and the number of individuals incorporated in the analysis. The optimum length for a transect was 250 m (Figure B.1.1 in Appendix B.1) and identified transects were spaced a minimum of 100 m apart to create individual sampling units. Transects with fewer than three fish present were removed to enable subsequent statistical analysis. The final number of transects analysed in this study was 55 (17 at Coral; 19 at Melville; 19 at Atlantis). Fish from 20 commercially important families (Rogers et al., 2017) were recorded per transect (Table 3.2), and all analyses were conducted at family level. Families with fewer than three observations were removed from the analysis.

As ROV speed differed across transects because of current-driven variations, and given that this study focuses on highly mobile species, observations were standardised by transect duration (obs/duration in hours) before calculating total abundance, richness (number of families), and Shannon diversity index for each transect.

Table 3.2: Commercially important fish families observed at Coral, Melville and Atlantis. The middle column includes species-level observations and the final column records ROV dives in which organisms from this family were observed. Families in bold font represent the 15 families that were retained in the analysis.

Family	Species	Common name	ROV dive no.
Berycidae (alfonsino)	*Beryx sp.* *Beryx splendens* *Centroberyx druzhinini*	Splendid alfonsino	4,5,7,15,17,18
Carangidae (amberjacks)	*Seriola lalandi*	Yellowtail amberjack	9
Centrolophidae (medusafish)	*Centrolophus niger* *Hyperoglyphe antarctica*	Yellowtail amberjack	9
Cyttidae (dories)	*Cyttus traversi*	King dory	8, 15

Etmopteridae (lantern shark)	*Etmopterus sp.* *Etmopterus spinax*	Lantern shark Velvet belly lanternshark	3, 4, 7, 8, 10, 15, 17
Gempylidae (escolars)	*Promethichthys prometheus*	Roudi escolar	1, 7, 17
Hexanchidae (cow shark)	*Hexanchus griseus*	Bluntnose sixgill shark	2, 17
Latridae (trumpeteers)	*Nemadactylus monodactylus*	St. Paul's fingerfin	9, 17
Moridae (morid cod)	*Guttigadus kongi* *Mora moro* *Guttigadus sp.* *Laemonema compressicauda* *Lepidion sp..* *Physiculus sp.* *Tripterophycis sp.*	Austral cod Common mora Morid cod	1, 2, 3, 4, 5, 7, 8, 9, 10, 15, 16, 17
Nototeniidae (antarctic cod)	*Dissostichus eleginoides*	Patagonian toothfish	1
Odontaspididae (sand shark)	*Odontaspis ferox*	Smalltooth sand tiger	9
Ophididae (cusk eel)	*Ophidiidae sp*	Cusk eel	5
Oreosomatidae (oreos)	*Allocyttus niger* *Neocyttus rhomboidalis* *Oreosoma atlanticum* *Pseudocyttus maculatus*	Black oreo spiky oreo Ox-eyed oreo Smooth oreo	1, 10, 15, 16, 17
Pentacerotidae (armourhead	*Pentaceros richardsoni*	Pelagic armourhead	15, 16, 17, 18
Polyprionidae (wreckfish)	*Polyprion americanus* *Polyprion oxygeneios*	Atlantic wreckfish Hapuku wreckfish	2, 7, 8, 9, 15, 17
Scorpaenidae (scorpionfish)	*Scorpaenidae sp.* *Scorpaena sp.*	Scorpionfish	7, 8, 9, 10, 15, 17
Scyliorhinidae (catshark)	*Apisturus sp.* *Bythaelurus naylori*	Ghost catsharks Dusky snout catshark	10, 17
Sebastidae (rockfish)	*Heliconus dactylopterus* *Trachyscorpia sp.* *Sebastes norvegicus*	Blackbelly rosefish Rockfish Rosefish	2, 4, 7, 8, 9, 15, 17
Squalidae (dogfish shark)	*Squalus mitsukurii*	Shortspine spurdog	15, 17, 19
Trachichthyidae (slimehead)	*Hoplostethus atlanticus*	Orange roughy	2, 4, 10, 15, 16, 17, 18

3.2.4 Environmental data

For each transect, descriptive parameters (site, depth, substrate type and distance to nearest ridge feature, oceanographic parameters) were extracted. Additionally, variables describing terrain structure and seascape composition and configuration in three different sizes of area (250 m, 500 m, 1000 m) surrounding transects, referreed to as 'buffer zones' in the remainder of this chapter, were quantified (Table 3.3).

Terrain structure was derived from bathymetric data at a raster cell resolution of 25 m x 25 m (Rogers & Taylor, 2012). Orientation, slope, terrain complexity (VRM, TRI) and curvature (including TPI) (Wilson et al., 2007) were quantified within a 3 x 3 moving window using R packages raster (Hijmans, 2017) and spatialEco (Evans, 2017) and the average value for each terrain derivative was recorded per transect (Table 3.3). Benthic seascape composition and configuration were measured using unsupervised benthic maps (Swanborn et al., 2022a)(Chapter 2), at a raster cell resolution of 25 m x 25 m. Briefly, to produce these maps geomorphological classes were determined through K-means classification in R v3.6.3 of depth-normalised terrain characteristics from 5 SWIR seamounts, including Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Bank and Atlantis Bank (using relative depth, slope, curvature, terrain complexity and aspect). Five geomorphological classes were identified and mapped out: seamount summit, ridges, slopes, NW flanks and SE flanks. Benthic maps were used to identify seascape composition (proportion of class types, their size, abundance, richness and diversity) and configuration (spatial configuration of class types, full list of metrics in Table 3.3) in multi-scale sample units extending 250 m, 500 m and 1000 m around each transect with Fragstats 4.2 (McGarigal et al., 2012) (Fig. 3.2). Fragstats is a spatial analysis program. It uses the areal extent and spatial distribution of patches (in this case, geomorphological classes) from categorical maps of landscapes (in this case, seascapes) to obtain measures of landscape structure (Table 3.3).

Collinearity between derived variables was analysed using the Spearman correlation index, and of variable pairs with a correlation $> |0.7|$, one variable was removed based on the variables' ease of interpretation. Measures of seascape composition and configuration were highly collinear between buffer sizes. To identify the appropriate

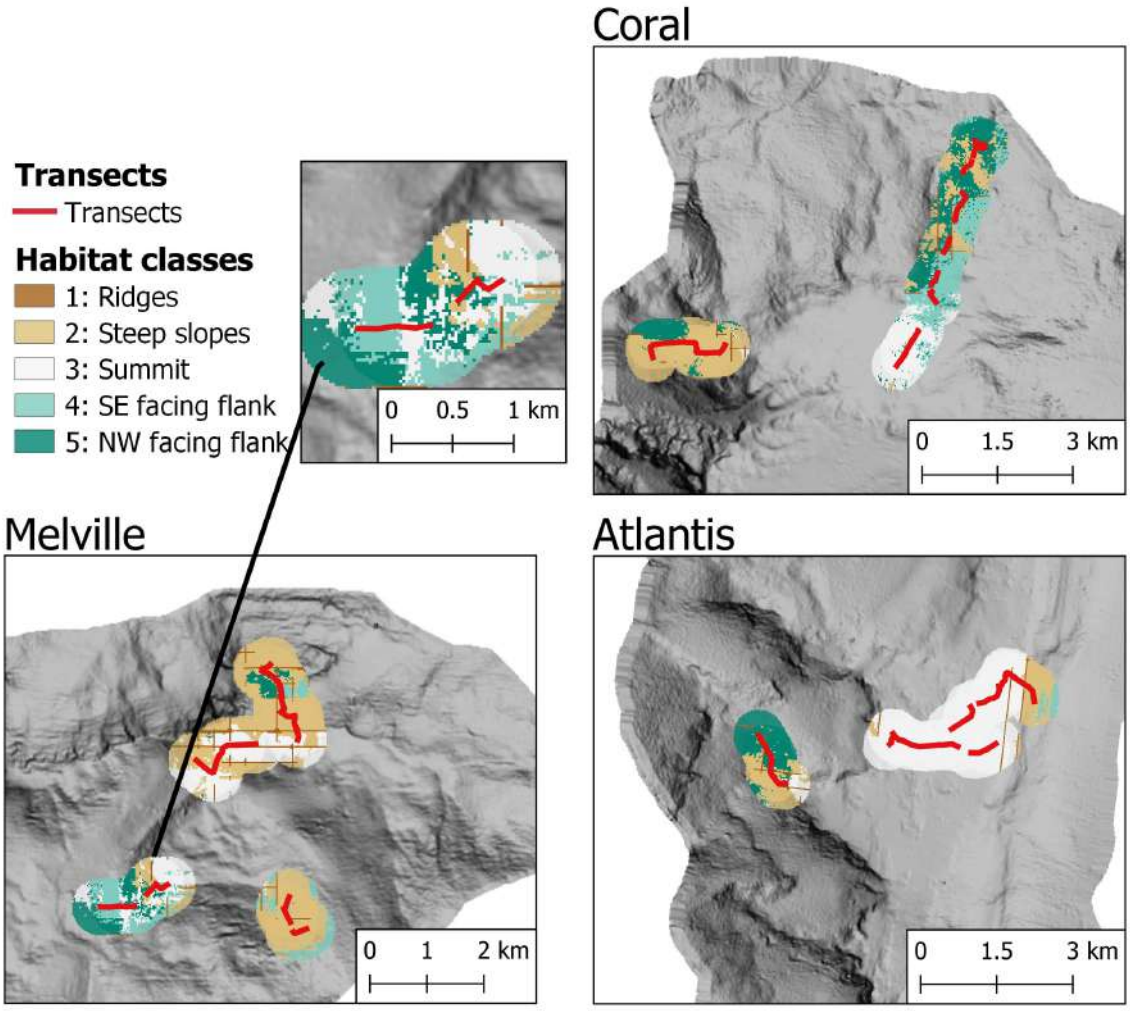


Figure 3.2: Spatial visualisation of environmental data extraction. 500 m buffers were created around the 250 m transects (red lines) and used to quantify seascape composition and configuration using the occurrence and spatial distribution of geomorphological classes (top left). Remaining panels show 500 m geomorpohlogical classes in buffers and 250 m transects plotted on hillshade maps of Coral, Melville and Atlantis.

scale of analysis, associations between biological metrics and the metrics extracted from the different buffer sizes. Metrics extracted from 500 m sampling units exhibited stronger correlation with family abundance, and were retained. A total of 18 variables describing environmental structure was used for analysis (Table 3.3).

Table 3.3: Measures of environmental structure explored for use in models, including abbreviated names used in the analysis where applicable. The final 18 variables are indicated.

Type	Metric	Description	Retained?	Scales
General	Site	Seamount name (Coral, Melville or Atlantis)	Yes	Transect average
	Depth	Continuous (m)	Yes	
	Distance to ridge feature (RidgeDist)	The closer to a ridge the higher the likelyhood of high productivity	Yes	
Oceanography	Temperature	Temperature (C)	No, highly collinear with depth (lower temperature with depth)	Transect average
	Salinity	Salinity (g per kg)	No, highly collinear with site (highest salinity at Coral)	
	Pressure	Pressure (bar)	No, highly collinear with depth (higher pressure with depth)	
Terrain structure	Slope	Slope angle (degrees)	Yes	Transect average
	Slope of slope	The change of the slope gradient, acts as a measure of terrain variability	No, highly collinear with VRM	
	Vector Ruggedness Measure (VRM)	Measure of terrain complexity	Yes	
	Terrain Ruggedness Index (TRI)	Local variation in seabed terrain, associated with changes in habitat complexity	No, highly collinear with slope and proportion of sloping terrain	
	Curvature	The orientation and relative elevation of the surface	No, highly collinear with TPI	
	Topographic Position Index (TPI)	Measure of curvature - indicates relative elevation	Yes	
	Aspect (eastness and northness)	Measures of terrain orientation	Yes	
Composition	Substrate type	Cold water coral, mesophotic reef, coral rubble, gravel, boulders, cobbles, bedrock, sediment veneer, mud	Yes	Transect average

	Proportion of habitat	Proportion of each patch type (summit, slope, SE flanks, NW flanks, ridges) in surrounding environment	Yes x4 (500 m buffer) apart from proportion of sloping habitat (highly collinear with slope and TRI)	Buffers (250 m, 500 m, 1000 m)
	Mean patch area (PatchArea)	Average size of patches in surrounding environment	Yes (500 m)	
	Patch abundance and richness	Measures of the number of patches present and the number of different types	No, highly collinear with Shannon evenness and diversity, patch area, landscape shape index, interspersion and juxtaposition and division index	
	Shannon Diversity	Diversity metrics incorporating the number of patch types and their relative abundance	No, highly collinear with Shannon evenness, landscape shape index and division index	
	Shannon Evenness		No, highly collinear with Shannon Diversity, landscape shape index and division index	
Configuration	Contagion	Extent to which patch types are aggregated or clumped. Higher values indicate increased aggregation	Yes (500 m buffer)	Buffers (250 m, 500 m, 1000 m)
	Mean Shape index (PatchShape)	Quantifies average shape of patches: higher values indicate more complex shapes.	Yes (500 m)	
	Mean Euclidan Nearest Neighbour (ENN)	Measure of average proximity between patches. Lower indicates more connected seascape	Yes (500 m)	
	Interspersion and Juxtaposition Index (Interspersion)	Measure of intermixing	Yes (500 m)	
	Landscape shape index (LandscapeShape)	Measure of patch disaggregation. Higher values indicate more disaggregation and internal edge	Yes (500 m)	
	Division index (Division)	Measure of splitting. Higher values indicate a more subdivided landscape.	No, highly collinear with landscape shape index, Shannon diversity and evenness and patch richness	

3.2.5 Analysis

All modelling and analysis was conducted in R version 4.0.3.

Assemblage composition with site and depth

To assess whether seamount assemblages differ between depth zones and seamount (geographic location), a PERMANOVA was conducted on the Bray-Curtis dissimilarity matrix over 999 permutations. The time-corrected abundance data matrix was fourth-root transformed before analysis to reduce the effect of dominant outliers such as abundant schooling fish (i.e. Polyprionidae, Oreosomatidae). Pairwise comparisons were performed post-hoc using the R package pairwiseAdonis (Martinez Arbizu, 2020). Additionally, indicator species analysis (Cáceres & Legendre, 2009) determined whether families exhibited significant associations with sites or depth classes. An nMDS (non-metric multidimensional scaling) plot was used to visualise compositional similarities in fish assemblages between transects.

Assemblage-level responses to seascape heterogeneity

Regression trees and random forests (Breiman, 2001) tested associations of assemblage characteristics (abundance, richness and diversity) with predictor variables. These approaches were chosen for their ability to explore potentially complex non-linear fish-seascape associations, including interactions between predictors.

Binary regression trees, implemented through R package rpart (Therneau & Atkinson, 2019) visualised the main structure of regression relationships. Trees for abundance, richness and diversity were fitted using 10-fold cross-validation and tree size (number of splits) was controlled by optimising the complexity parameter (cp) value to maximise cross-validation accuracy with high R squared values. Random forests, implemented using R package RandomForestSRC (Ishwaran & Kogalur, 2021), assessed the importance and influence of predictor variables on assemblage characteristics. Models were implemented by bootstrapping without replacement and tuned to minimise the cross-validated prediction error (out-of-bag or OOB error) by setting the optimum number of variables selected as candidates for splitting node (mtry) and the minimum

size of the terminal node. The OOB data was used for a performance assessment using variance explained (R Squared) and the error rate. Confidence intervals evaluating the change in Mean Squared Error over 200 random permutations assessed variable importance, with significance tested at the alpha=0.05 level (Breiman, 2001). Partial-dependenc plots subsequently showed the response of assemblage characteristics to significant predictor variables. Variable interactions were tested using maximal subtree analysis (Ishwaran & Kogalur, 2007).

Fish family responses to heterogeneity

As individual fish families may have specific habitat associations (e.g. Moore et al. (2016), multivariate alternatives of regression trees and random forests were applied to test whether families are associated with particular combinations of environmental variables. Multivariate regression trees (MRTs) (De'ath, 2002), implemented using R package mvpart (De'ath, 2014), explored, explained and predicted relationships between multispecies data and environmental characteristics. They were constructed using 10-fold cross-validation, and the optimum tree size was chosen using the lowest value for the relative cross-validated error.

Multivariate random forests (MRFs) (Segal & Xiao, 2011), implemented using the package RandomForestSRC (Ishwaran & Kogalur, 2021), extended MRTs with subsampling techniques from random forests. MRFs were constructed using bootstrapping without replacement and tuned the number of candidates for splitting node (mtry) and the minimum size of the terminal node. Model performance was assessed using the mean OOB prediction error (standardised mean squared error) and average OOB variance. Ten model resamples repeating this process were created to assess precision.

For each family, the model resample with the lowest mean squared error was selected to calculate confidence intervals of variable importance over 200 random permutations, similar to traditional random forests. The five most important variables were recorded for each family and partial dependence plots showed fish family responses to these variables. The number of times each variable occurred as one of the five primary drivers was recorded to identify the relative importance of terrain structure, composition,

and configuration metrics. Finally, variable interactions were tested using maximal subtree analysis (Ishwaran & Kogalur, 2007).

3.3 Results

3.3.1 Assemblage composition with site and depth

The final modelling dataset contained 1053 fish observations including at least 47 unique taxa from the 15 commercially important families. The most abundant families were the Polyprionidae (wreckfish, n=270), followed by the Moridae (morid cod, n=216), Oreosomatidae (oreos, n=133), Latridae (trumpeteers, n=124), Squalidae (dogfish sharks, n=110), and Pentacerotidae (armourheads, n=81). The most widespread families, measured as the number of transects in which they were present, were the Moridae (n=44), Scorpaenidae (scorpionfishes, n=20), Sebastidae (rockfishes, n=18) and Oreosomatidae (n=16).

The PERMANOVA revealed significant differences in fish assemblages between depth zones (epipelagic, mesopelagic and bathypelagic), sites, and interaction effects between site and depth, with the majority of variance attributed to site effects (40%) (Table B.2.1 in Appendix B.2). Pairwise comparisons (Table B.2.2 in Appendix B.2) showed that assemblages differed significantly between all sites ($p < 0.05$), with the strongest differences between Coral Seamount and Atlantis Bank. Further, pairwise comparisons between depth zones (Table B.2.3 in Appendix B.2) showed that assemblages differed significantly ($p < 0.05$) between the epipelagic and bathypelagic zone and between the epipelagic and mesopelagic zone (defined in Table 3.4), but not between the mesopelagic and bathypelagic zone.

Indicator species analysis showed that the majority of families (10 out of 15) in the modelling dataset were significantly ($p < 0.05$) associated with a site and/or a depth zone (Table 3.4). These findings were apparent in the nMDS (Fig. 3.3), which showed that fish abundance was driven by site and depth as well as family associations.

Table 3.4: Associations of family occurrence with site and depth zone. Bold font and star indicate significant association

Site	**Families**
Coral	**Moridae***
Melville	**Carangidae***, Etmopteridae, **Latridae*, Polyprionidae*, Scorpaenidae*, Sebastidae***
Atlantis	**Berycidae***, Centrolophidae, Gempylidae, Hexanchidae, **Oreosomatidae*, Pentacerotidae*, Squalidae***, Trachichthyidae
Depth Zone	**Families**
Epipelagic (0-200 m)	**Carangidae*, Latridae*, Polyprionidae*, Scorpaenidae*, Sebastidae***
Mesopelagic (200 m-1000 m)	Berycidae, Centrolophidae, Gempylidae, Pentacerotidae, Scorpaenidae, Sebastidae, Squalidae
Bathypelagic (>1000 m)	Etmopteridae, Hexanchidae, Moridae, Oreosomatidae, **Trachichthyidae***

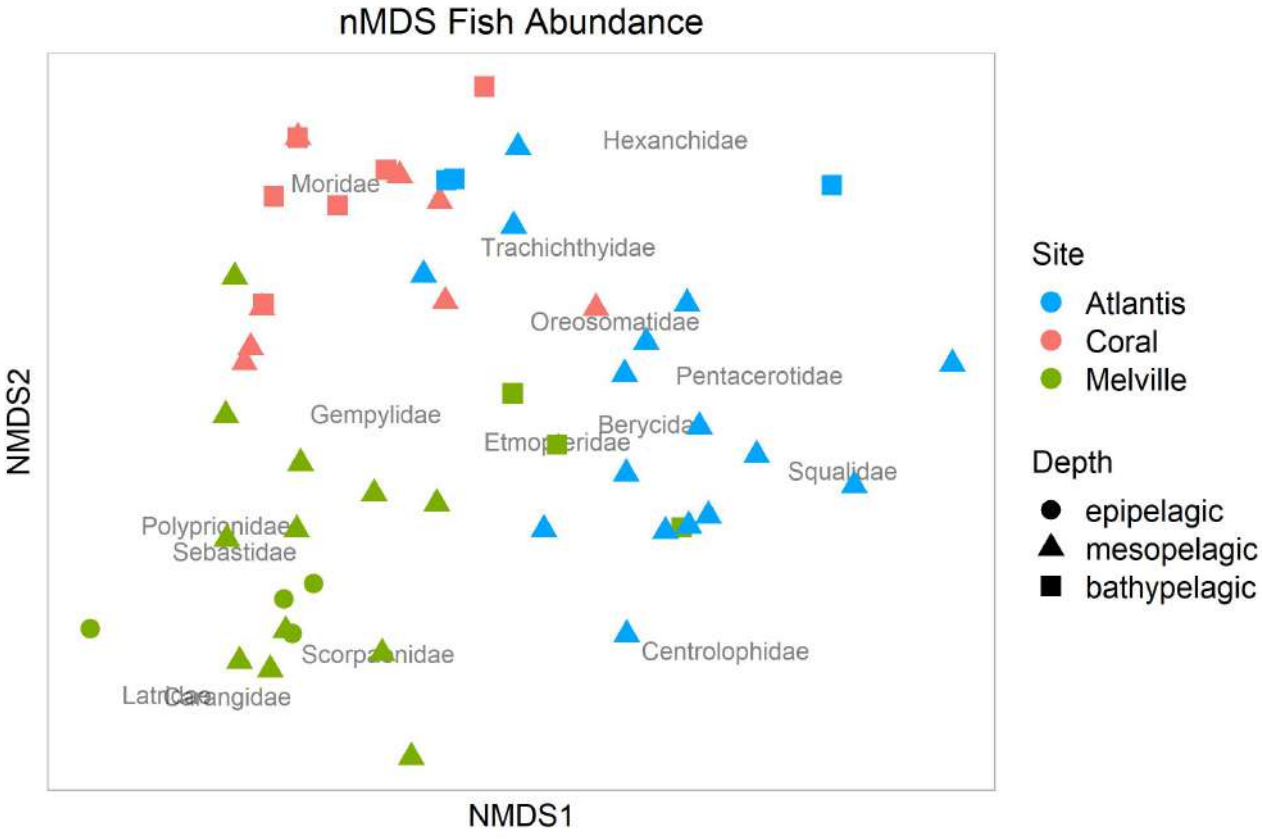


Figure 3.3: nMDS (stress=0.08) conducted on standardised fish abundance data confirming site- and depth driven separation of assemblages

3.3.2 Assemblage-level responses to heterogeneity

Regression trees (Fig. 3.4) explained 87% of variation in abundance and 77% of variation for both richness and diversity, but had cross-validated errors of over 50%. This indicates high explanatory power, but limited predictive power. The influence of the main splitting parameters was identified by random forests (Fig. 3.5), which explained 40.73% of variation in abundance, 42.3% of variation in richness and 52.75% of variation in diversity, but equally had higher error rates. The main driving variables of assemblage characteristics are depth, site, the proportion of summit and the proportion of ridge, patch shape and landscape shape.

Fish abundance (Fig. 3.4a) is strongly dependent on depth, with shallower areas ($<$ 400 m depth) characterised by highest abundances. At mesopelagic and bathypelagic depths, more complex patch shapes support higher abundance. For simpler patch shapes substrate characteristics are important, and patches with gravel, coral rubble or cold-water coral host higher abundances than patches with boulders and sediment veneer or mud. Random Forests (Fig. 3.5a,b) confirmed a strong dependency of abundance on depth and a positive association with complex patch shapes and disaggregated seascapes. Some evidence of variable interactions were observed (Fig. B.3.1 in Appendix B.3) between Depth and Patch Shape.

Family richness (Fig. 3.4b) is driven by site, and transects surveyed at Coral host lower richness than Atlantis and Melville. At Atlantis and Melville, areas with higher proportions of summit, high structural complexity and complex patch shape support highest richness. For transects with a lower proportion of summit, the proportion of ridge terrain positively influences richness. Random Forests Fig. 3.5c,d) confirmed lowest richness at Coral, and positive associations with an increased proportion of summit and ridge terrain and complex patch shapes. They additionally showed an effect of depth, with higher family richness in shallower transects. There was no evidence of interactions between variables included in the model (Fig. B.3.2 in Appendix B.3), apart from weak ties between Site and the proportion of summit.

Shannon diversity (Fig. 3.4c) is equally site-dependent, with higher diversity in the transects surveyed at Atlantis and Melville than at Coral. At Atlantis and Melville,

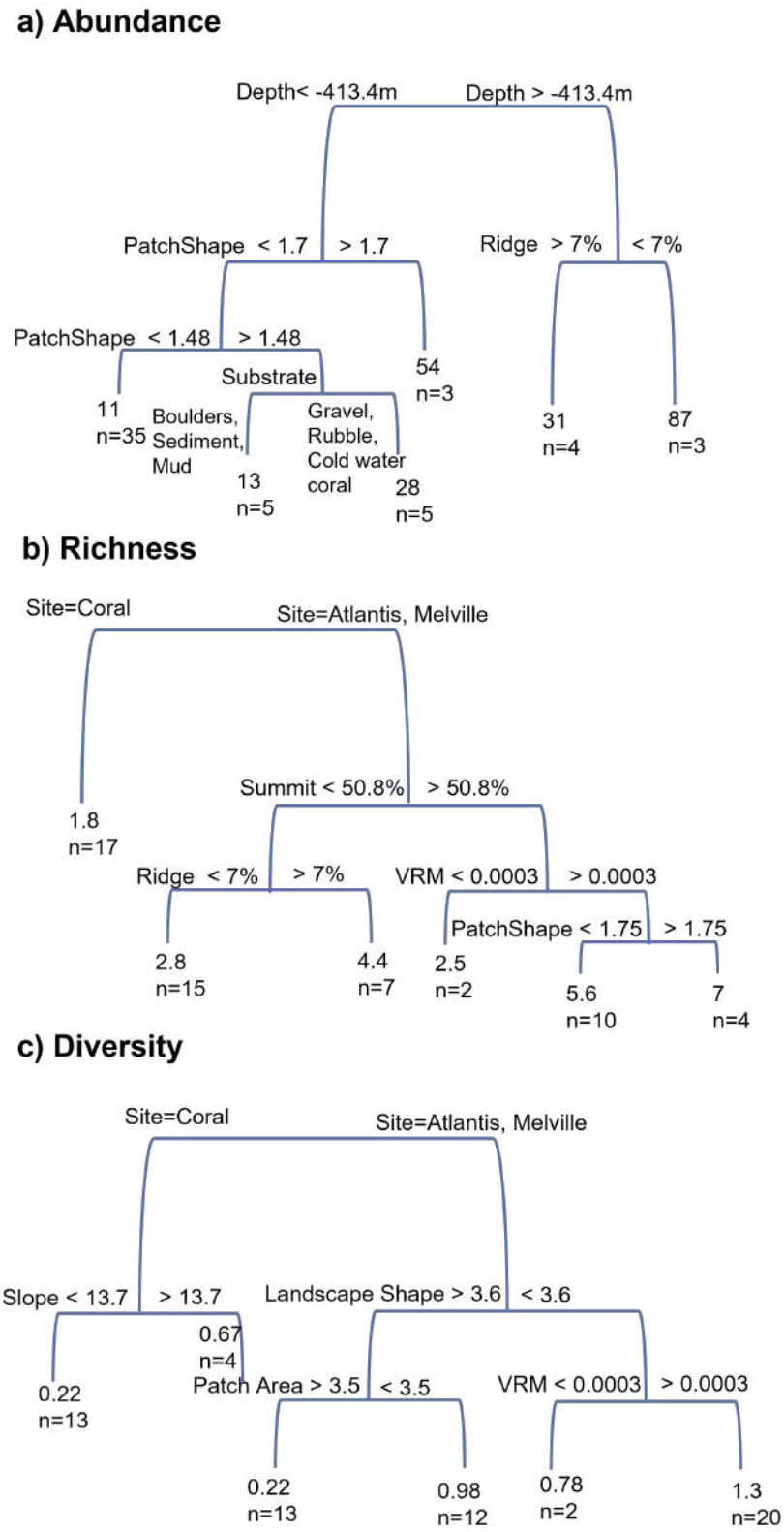


Figure 3.4: Regression trees for abundance (a), richness (b) and diversity (c). Splits indicate important breaks in variable values, whereas end nodes indicate average abundance, richness and diversity values and the number of observations in that split.

more aggregated landscapes with high structural complexity host highest diversity, followed by more diverse landscapes with small patch areas. At Coral, diversity is higher in more sloping areas. Random forests (Fig. 3.5e,f) revealed an additional effect of the proportion of summit terrain and a positive association with the proportion of ridge terrain. However, resampled variable importance confidence intervals revealed that only site, proportion of summit and landscape shape were significant ($p < 0.05$) drivers. No variable interactions were observed (Fig. B.3.3 in Appendix B.3), apart from weak ties between site and landscape shape (simpler landscape shapes at Atlantis).

3.3.3 Family-specific responses to heterogeneity

Multivariate regression trees on untransformed family abundance data (Fig. 3.6) explained 74% of variation, but, like the single regression trees, had low predictive power. Primary splits (depth, patch shape, proportion of ridge and summit and site) matched those obtained for the univariate variables.

Multivariate random forests modelled the effects of measures of heterogeneity on individual families. Across families, MRFs explained an average 34% of variance, but had low predictive power indicating results do not readily generalise. Model performance (Fig. 3.7) varied between families and depth zones. Overall, model performance was best (higher variance explained, lower error rate) for epipelagic and mesopelagic families occuring in higher abundances (Latridae, Carangidae, Polyprionidae, Pentacerotidae, Squalidae). Most families for which reduced model performance was observed (Etmopteridae, Centrolophidae, Hexanchidae, Gempylidae) were bathypelagic and had a lower number of observations in the modelling dataset. As fish occurrence is heavily influenced by heterogeneity of oceanographic parameters in addition to terrain parameters, family models with variance explained of over 30% were deemed acceptable (Berycidae, Carangidae, Latridae, Moridae, Oreosomatidae, Pentacerotidae, Polyprionidae, Sebastidae, Squalidae,) following similar values in shallow reef studies (Costa et al., 2014; Pittman et al., 2009). Associations with seascape composition, configuration and terrain structure were assessed per depth class.

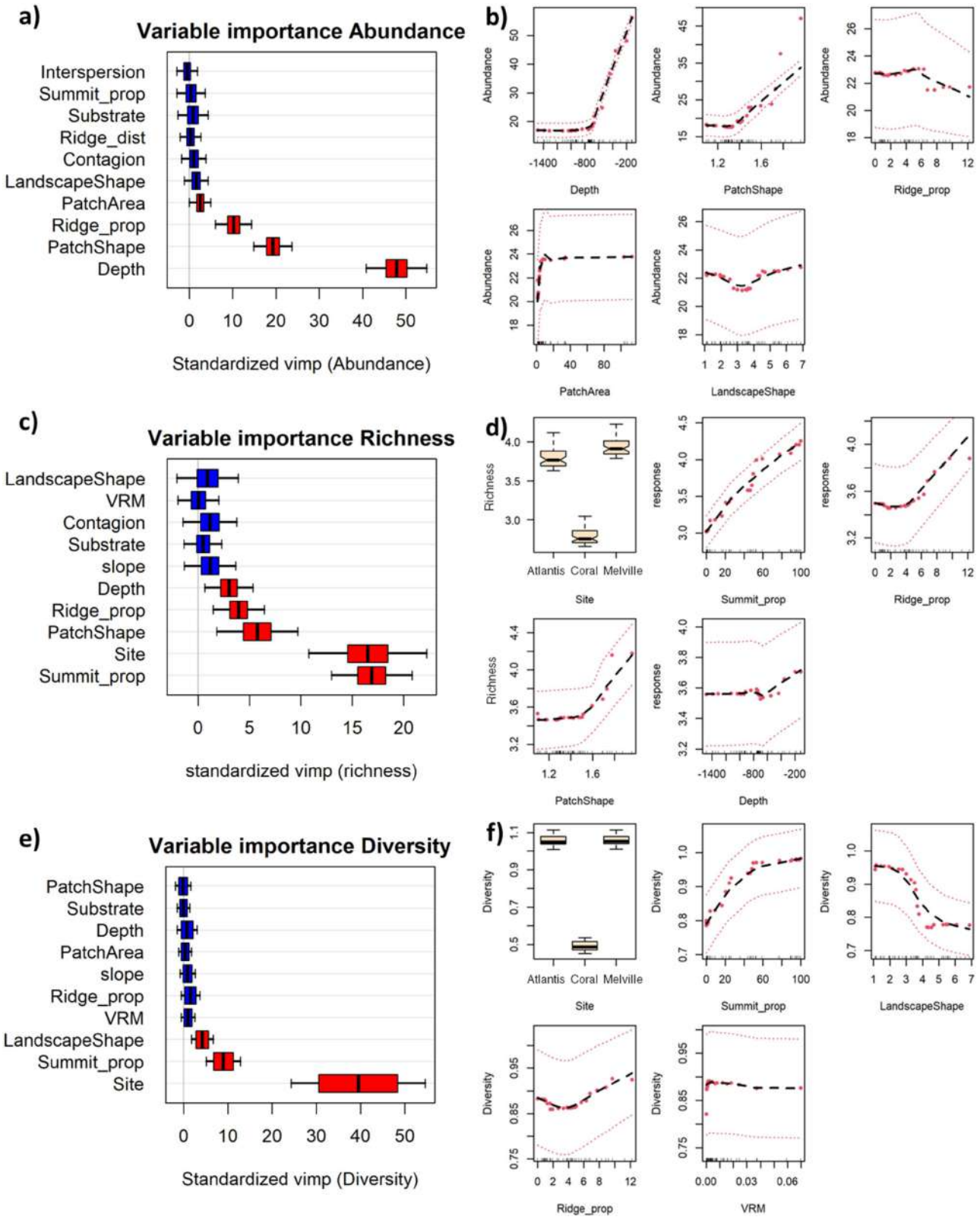


Figure 3.5: Importance and effect of seascape heterogeneity on abundance (a,b), richness (c,d) and diversity (e,f). Left-hand panels indicate variable importance (vimp) of the 10 main variables obtained through resampling, with red colours indicating a significant ($p<0.05$) effect. Right-hand plots show partial responses to the main 5 (including significant) parameters, where black dashed lines and red points indicate the partial values, and the dashed red lines indicate an error bar of two standard errors.

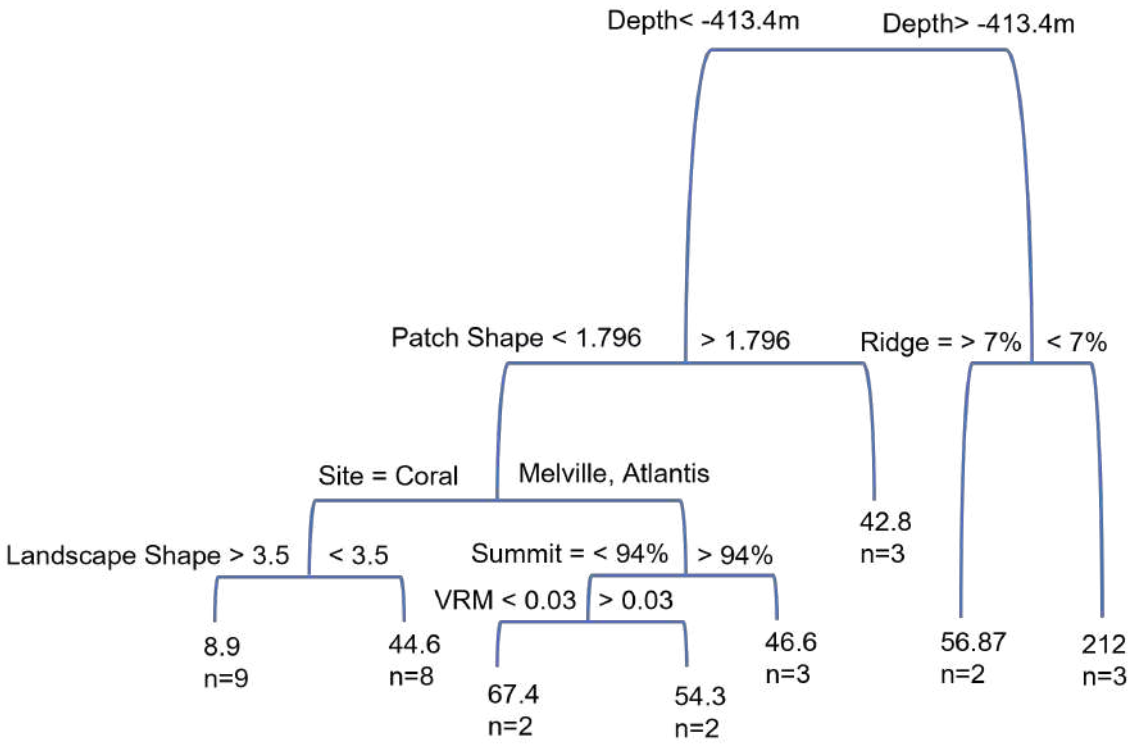


Figure 3.6: Multivariate regression tree of fish family abundance. Splits indicate important breaks in variable values. End nodes indicate average abundance and the number of observations in that grouping.

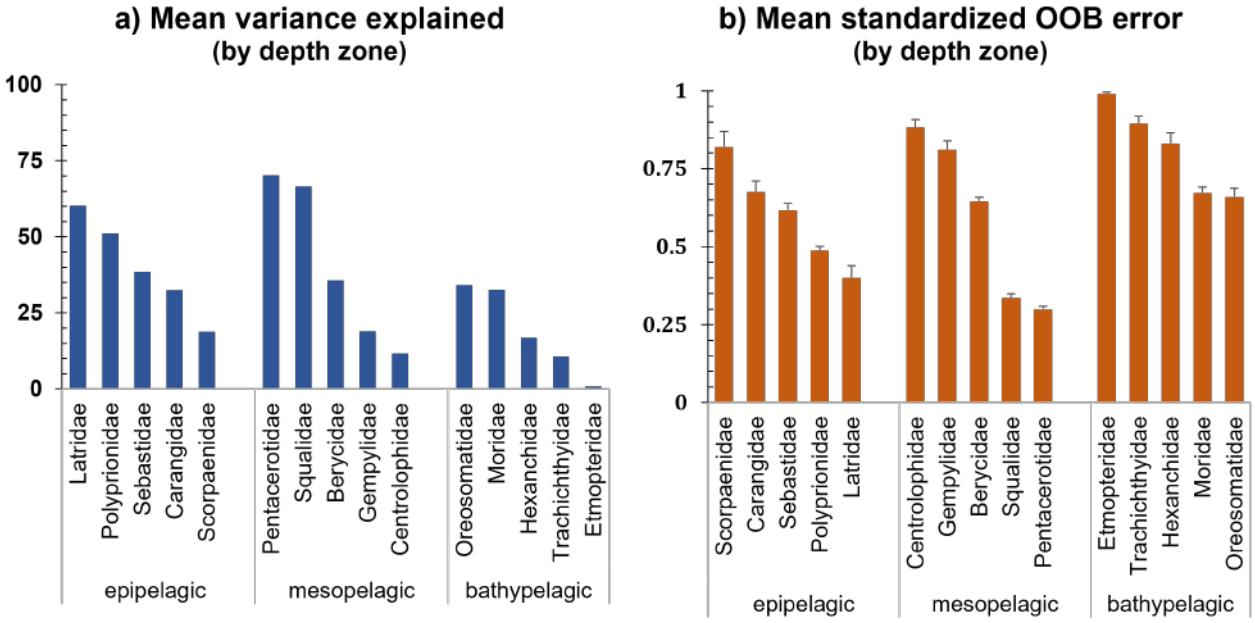


Figure 3.7: Model performance of multivariate random forests measured by variance explained (a) and standardized out-of-bag error (b). Error bars represent standard deviations over 10 model resamples.

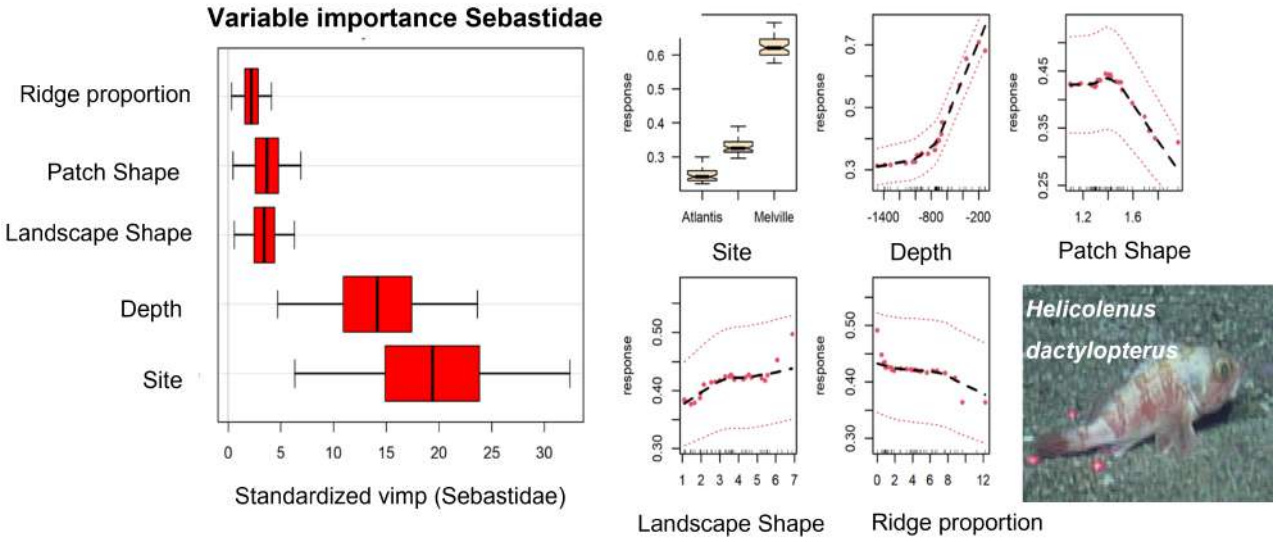


Figure 3.8: Example output of importance and effect of predictor variables for Sebastidae. The left-hand panel indicates the 5 main driving variables obtained through resampling, with red colours indicating a significant ($p < 0.05$) effect. The right-hand plot shows partal responses to these main 5 parameters with 95% confidence intervals. Outputs for other families can be found in Appendix B.4

Families associated with the epipelagic zone were Carangidae, Latridae, Polyprionidae, Scorpaenidae and Sebastidae (example of plots are given for Sebastidae Fig. 3.8). Variable importance plots for these families (Fig. B.4.1 and B.4.2 in Appendix B.4) revealed a combined effect of site and depth with Melville Bank the only site where the epipelagic zone was surveyed. Seascape composition also positively affected abundance, with the proportion of slope and ridge terrain driving abundance. For Latridae, substrate type (mesophotic reef) was also important. Of the configuration metrics, patch shape was important for Sebastidae (Fig. 3.8), indicating a role of spatially simple patch types.

Families associated with the mesopelagic zone were Pentacerotidae, Squalidae, Berycidae, Gempylidae and Centrolophidae (Fig. B.4.3 and B.4.4 in Appendix B.4). Families were mainly affiliated with transects at Atlantis Bank and showed a positive association with the summit. There was a strong role for configuration metrics with abundance increasing with increased patch area (Pentacerotidae, Centrolophidae), complex patch shapes (Pentacerotidae, Squalidae) and aggregated landscape shapes (Pentacerotidae, Squalidae, Berycidae, Centrolophidae). Some families (Pentacerotidae, Centrolophidae, Gempylidae) also appeared dependent on complex patch shapes.

Families associated with the bathypelagic zone were Etmopteridae, Hexanchidae, Moridae, Oreosomatidae and Trachichthyidae (Fig. B.4.5 and B.4.6 in Appendix B.4). Only models for Oreosomatidae and Moridae had reliable performance. Across families there was a dependence on site and depth, with families at Atlantis Bank (Trachichthyidae, Oreosomatidae, Hexanchidae) associated with increased proportions of ridge terrain and/or reduced summit proportion. Effects of configuration metrics were mixed, but small patch areas (Oreosomatidae, Etmopteridae), increased contagion (Moridae, Etmopteridae), landscape clumping (Moridae, Hexanchidae) and complex patch shapes (Hexanchidae, Oreosomatidae) were influential.

Summing the times that each variable appeared in the main five predictor variables of each family (Fig. 3.9), key variables were site and depth, followed by configuration measures (landscape shape, patch shape and patch area), and composition measures (proportion of summit, ridge and flank). The importance of terrain metrics (VRM, TPI, northness and eastness) was reduced. Limited predictor interactions were found in the maximal subtree analysis (Fig. B.3.4 in Appendix B.3) for Depth, Landscape Shape and Patch Shape.

3.4 Discussion

3.4.1 Fish assemblages with site and depth

Assemblage composition differed between the transects surveyed on each seamount. Fish abundance, diversity and richness was lowest in the transects surveyed at Coral Seamount and few of the families found at other sites were found here. Melville Bank was the shallowest seamount surveyed, with a summit hosting a high abundance of predatory fish including amberjacks, wreck fishes and trumpeteers. The summit of Atlantis Bank was deepest, but transects surveyed at this site hosted high fish diversity, richness and abundance, including oreos, pelagic armourhead and orange roughy.

These differences in faunal composition may be explained by the highly dynamic and variable oceanographic conditions created by the Agulhas Return Current, the Subtropical Front, and the Sub-Antarctic Front (Rogers et al., 2017) influencing the

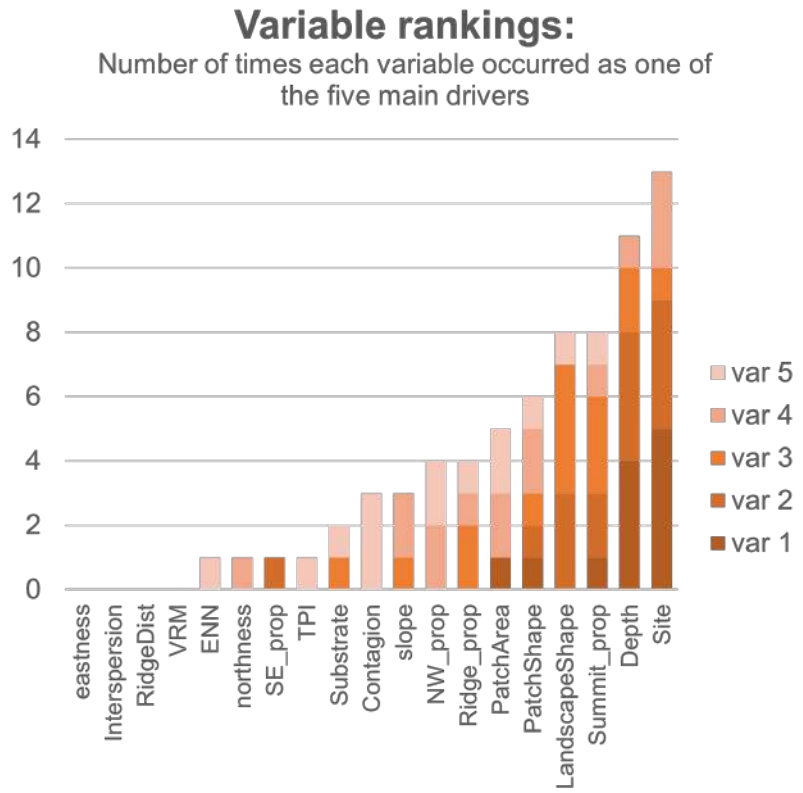


Figure 3.9: Variable rankings (number of times each variable occurred as one of the five main drivers) obtained from multivariate regression trees

geographic distribution of surveyed fish families. Oceanographic conditions at Coral Seamount, represented in the analysis by the variable 'depth', were strongly different from the other sites. It was the only seamount located in cooler, more saline and oxygenated Sub-Antarctic waters close to the Sub-Antarctic Front and south of the Agulhas Return Current and Subtropical Front (Pollard & Read, 2017). Melville Bank is located just north of the Subtropical front and Agulhas Return Current, and therefore exposed to dynamic conditions that can vary between Subtropical and Subantarctic. Additionally, its summit extends into the epipelagic zone and provides unusual and isolated shallow water habitat compared to the surrounding ocean, explaining the occurrence of mesophotic coral ecosystems and the high abundance of fish also found in shallow reef environments. Atlantis is located further northeast in the Subtropical Anticyclonic gyre. It experiences weak eddy currents and semi-diurnal upwelling creating varying productivity patterns (Read & Pollard, 2017), likely important for the high diversity of the found fish communities. It is notable

that observations on the biodiversity of pelagic species across the studied section of the South West Indian Ridge showed similar division of communities attributed to water mass variation from bacterioplankton to micronekton (midwater shrimps and gnathophausiids, cephalopods) and nekton (cephalopods; Djurhuus et al. (2017); Laptikhovsky et al. (2017); Letessier et al. (2017).

Knowing that survey depth is a major driver of deep-sea biodiversity and correlated with parameters as temperature and pressure (Table 3.3), the varying average site survey depth may further emphasise some of the broad-scale biological patterns found.

3.4.2 Responses to seascape heterogeneity

Fish-habitat associations were mainly driven by depth and site, but seascape metrics (composition and configuration) proved useful to describe habitat associations at studied locations in more detail.

Seascape composition

Seascape composition, the type and abundance of different broad-scale geomorphological classes (summit, ridge, slope, flanks), strongly influenced fish assemblages. The proportion of summit terrain was particularly important. At Coral Seamount and Melville Bank, higher proportions of summit terrain were associated with higher richness and diversity - noting the summit of Coral Seamount was not as extensively surveyed as those of Melville and Atlantis-, and at Atlantis the abundance of multiple families (Berycidae, Pentacerotidae, Squalidae) was dependent on the proportion of summit. In other geographic areas, seamount summits have also been shown to host higher biological abundance, richness and diversity than other parts of the seamounts (González-Irusta et al., 2021; Porteiro et al., 2013). Processes operating on seamount summits are different from those on flanks, for example the exposure to hydrodynamic processes and resulting nutrient availability (Clark et al., 2011; White et al., 2007), potentially causing community differences as identified here.

The second important geomorphological class was the proportion of ridge features. Local topographic elevations such as ridges and crests have been demonstrated to

positively benefit fish biodiversity (Leitner et al., 2021), but our results only partly matched those observations. A higher proportion of ridge features was positively correlated with richness, but did not significantly affect abundance or diversity. However, ridges were a key determinant of the abundance of several individual families (Carangidae, Oreosomatidae, Scorpaenidae, Trachichthyidae). The partial effect of ridge terrain may be related to the fact that, as for summits, ridges did not receive equal survey effort across sites. Additionally, the spatial resolution at which benthic maps were produced may not be appropriate for all surveyed assemblages (Kendall et al., 2011), being too broad to directly link with assemblages.

Despite the importance of steeply sloping terrain for biodiversity through possible current amplification and effects on nutrient availability (Leitner et al., 2021), the analysis did not reveal a clear effect of these features on demersal fish assemblages, apart from at Coral where steeper slope gradients were correlated with higher diversity. Similar to slope, the proportion of flank terrain did not appear to influence assemblage characteristics. When flank terrain occurred in the top five driving variables for families (Gempylidae, Carangidae, Latridae, Hexanchidae), abundance had a negative association with the proportion of flank habitat suggesting that flanks hosted lower abundances of fish. However, flank terrain was only extensively surveyed at Coral, where overall fish abundance, diversity and richness were lower than at the other sites. A more extensive survey of flanks at Melville Bank or Atlantis Bank might support a more reliable assessment of the importance of flank habitat. Assemblages on flanks may show high specificity and diversity because of taxa only found at deeper depths (González-Irusta et al., 2021). Flank habitats are also more prone to trawling than other parts of the seamounts, which might further influence fish assemblages. Video observations confirmed historical or ongoing fishing activity at all three seamounts (Rogers & Taylor, 2012; Woodall et al., 2015).

It is important to recognise that benthic maps were created without ground-truthing benthic assemblage occurrence or substrate types and instead are based on geomorphological characteristics of the terrain. Backscatter was not included as predictive variable as data quality was poor for Coral and Melville (see also Chapter

2). Although substrate types were captured as separate predictive variables in the analyses, incorporating ground-truthing or backscatter in the production of benthic maps may provide a more detailed view on the effect of habitat composition and configuration on demersal fish.

Seeascape configuration

Incorporating configuration metrics helped assess the effects of patch area, patch shape and seascape aggregation on fish assemblages and individual families.

Larger patch sizes were expected to positively influence abundance. On land, many species have minimum patch size requirements (Godron, 1981), which also appear important for demersal fish species (Anderson et al., 2009). A positive relationship between patch area and abundance was found for some summit-associated aggregating fish families at Atlantis (Pentacerotidae, Centrolophidae). These larger patch areas indicate increased availability of spatially continuous summit terrain, and support larger feeding aggregations. In contrast, assemblage diversity and some bottom-dwelling mesopelagic and bathypelagic families (Etmopteridae, Gempylidae) relate to small patch areas in more aggregated seascapes. These results fit the perspective of niche theory, which predicts more diverse and connected seabed environments support higher biological diversity (Harris, 2012; Ismail et al., 2018) This might be relevant for bottom-dwelling families that utilise their local environment for different activities (e.g. feeding, resting).

More complex patch shapes were expected to negatively influence fish assemblage characteristics due to edge effects: the abrupt changes in physical structure at the transition zones between patch types. Indeed, away from the summit, rockfish and scorpionfish (Sebastidae, Scorpaenidae) were associated with simple patch shapes. These solitary fish are bottom-dwelling and have low activity levels, and therefore might depend on contiguous environmental conditions. In contrast, complex patch shapes positively influenced abundance and richness of several other families . This matches literature from coastal habitats, suggesting that fish biodiversity may show positive responses to edges (Boström et al., 2011). In seamount environments, complex

patch shapes may, for example, be linked to the presence of complex shaped crest and ridge features, important for several demersal fish species by promoting exposure to nutrient-rich currents (Read & Pollard, 2017). Additionally, more complex patch shapes may create a more heterogeneous environment, that following niche theory, would be positively related to richness and diversity.

Aggregated landscape characteristics were expected to positively influence abundance because of structural connectivity provided by spatial continuity (Grober-Dunsmore et al., 2007). Indeed, spatial continuity, measured by the landscape shape index, was the main configuration metric influencing fish families and overall abundance and diversity. It is important to reiterate that the landscape shape index was highly collinear with landscape diversity, evenness, patch abundance and richness, and splitting index, and therefore also functions as a proxy of these metrics. The effect of landscape shape index varied between families, which also explains the non-linear relationship of landscape shape to overall fish abundance. Spatially contiguous seascapes appeared mainly important for the mesopelagic fish families found at Atlantis (including Pentacerotidae, Squalidae, Berycidae, Centrolophidae). These families dwell over summits for feeding and/or hunting, and increased availability of spatially contiguous summit terrain might therefore support larger abundances of these families. In contrast, bottom-dwelling Sebastidae appeared correlated to higher values of the landscape shape index. These indicate increased patch richness, and bottom-dwelling families might benefit from multiple patch types in their direct surroundings to support their low activity levels. Similarly, higher values of contagion and nearest neighbour index were important for bottom-dwelling Moridae at Coral Seamount, that use multiple habitats and may benefit from increased proximity of these habitats.

Interpreting fish-habitat associations using seascape metrics requires consideration of scale-dependent responses. Broad-scale geomorphological maps were deemed appropriate as many of the fish families targeted for fishing are highly mobile and use their environment over extended areas (Shotton, 2006). However, producing habitat maps at scales ecologically relevant for the fish families might further improve knowledge gained. For example, “summit” was classified as one feature, but within the broad-scale

summit feature there can be features such as boulders that might be ecologically relevant for some species (Bo et al., 2021). This study did not account for such finer scale interactions, as the resolution of the input data did not allow to resolve such detail. However, "substrate type" was incorporated at a finer scale (average of photo frames within transects) as fine-scale substrate features have been shown to strongly influence deep-water fish communities (Quattrini et al., 2012; Ross & Quattrini, 2007) but was not a major predictive variable. Finer scale mapping approaches, such as AUV mounted MBES could provide seascape maps at higher resolution and help delineate finer scale features corresponding to the habitat use of families under consideration (Lacharité & Brown, 2019; Proudfoot et al., 2020; Robert et al., 2017).

3.4.3 Final considerations

Importance

Conservation and fishery management of remote deep-sea ecosystems such as seamounts rely partly on proxies of habitat suitability to estimate ecologically important areas (Clark et al., 2012; Moore et al., 2016). This study highlighted that regional ecologically-relevant physical variables (e.g. temperature, salinity, dissolved oxygen, depth) determine the boundary conditions for more local effects of seascape composition, configuration and terrain structure on fish assemblages. A previous hierarchical biophysical classification of seamounts incorporating summit depth in the southern Indian Ocean already identified different classes along the SWIR, with Coral, Melville and Atlantis belonging to different groups (Clark et al. (2011); see also Sutton et al. (2017) for the mesopelagic), confirmed by this study.

At the scale of individual seamounts, current frameworks in seamount management already recognise the importance of particular broad-scale habitats – seascape composition-, such as the summit (Clark & Dunn, 2012). This study indicates the spatial characteristics and configuration of these habitats, in particular their shape and spatial continuity, are equally ecologically important. Considering spatial configuration could be valuable to achieve a representative network of protected areas incorporating seamounts varying in spatial characteristics of morphology (Clark

et al., 2011). Methodologically, this study also demonstrated that patch-based metrics provided a strategy to test new hypotheses related to species diversity in the deep sea, although this study did not provide conclusive results. Additionally, patch-based metrics had larger predictive power than continuous terrain metrics commonly used in developing proxies for deep-water biodiversity. The geomorphological class map from which composition and configuration metrics were derived in this study, was however constructed based on geomorphological characteristics, which incorporate terrain structure.

Study limitations

Although seascape composition, configuration and terrain structure proved useful to disentangle fish-habitat associations with different sets of environmental characteristics, they were derived from a limited number of observations and highly site-specific. This was indicated by the differences in performance of random forests and regression trees. Whereas both exhibited high explanatory power, predictive power was limited, limiting universal conclusions on the effect of seascape composition and configuration on seamount-associated fish. Although we recommend further adoption of seascape metrics, the lack of extensive surveys on all seamount geomorphological classes in this study limited the ability to identify assemblages and their drivers on seamount flanks. Future studies using more extensive groundtruthing surveys sampling representative classes and with a spatially balanced design can likely expand on this knowledge. Further, finer-scale data, both in taxonomic resolution and spatial resolution might provide additional insight in characteristics important for individual species targeted by fisheries. Indeed, finer scale taxonomic data may be more accurate for deep-sea habitat suitability modelling (Bowden et al., 2021) and fish-habitat associations are dependent on spatial scale and environmental context (Anderson et al., 2009).

3.5 Conclusion

As few seamount ecosystems have been studied in detail, there remains a need to increase our understanding on how seamount habitat heterogeneity supports biology and ecology

(Rogers, 2018). Using seascape ecology metrics rarely used in deep-water environments to study fish-habitat associations at SWIR seamounts, this chapter revealed:

1. Fish assemblages were primarily driven by depth and site, and seascape composition, configuration and terrain structure explained associations within sites and depth classes

2. Demersal fish responded to unique combinations of seascape composition, configuration and terrain structure depending on their traits, with some overlap between families found in the same sites and depth zones.

3. Broad-scale geomorphological classes, specifically the summit and the proportion of ridge terrain, and their spatial continuity and shape, were main drivers of assemblage characteristics

4. Metrics of seascape composition and configuration had higher explanatory power than commonly used terrain structure metrics.

Author contributions

A modified version of this chapter is under review at *Deep Sea Research Pt 1: Oceanographic Research Papers* as: Denise Swanborn, Veerle Huvenne, Thomas Malpas, Simon Pittman, Alex Rogers, Michelle Taylor and Lucy Woodall. *Seascape heterogeneity drives of Southwest Indian Ridge seamount-associated fish.* Author contributions are as follows:

DS- conceptualisation, methodology, formal analysis, writing – original draft, writing-review & editing. TM: data curation (fish ID), writing-review & editing. ADR: Funding acquisition, field data collection, data curation (fish ID), writing-review & editing. VH, SP, LW: supervision, writing-review & editing. MT: Field data collection, writing-review & editing.

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4 Geomorphological drivers of deeper reef habitats around Seychelles

Abstract

Mesophotic (30-150 m) and rariphotic (150-300 m) deeper reef habitats are important from an ecological and conservation perspective, yet remain understudied. Key knowledge gaps exist on the environmental patterns and processes that drive and shape their geographical distributions. Understanding these is particularly important for regions as the Western Indian Ocean, where deeper reefs are poorly studied but support food security and host economically important species. Spatial predictive models of assemblage occurrences, using terrain variables as predictors, offer a solution to address geographical gaps in our knowledge of deeper reef distributions.

This chapter identifies relationships between seafloor geomorphology, quantified at multiple scales using terrain metrics, and sessile benthic assemblages in four atoll seascapes in Seychelles using terrain models derived from high-resolution multibeam sonar and underwater video surveys. Using Random Forests and Boosted Regression Trees, this study demonstrated that terrain derivatives extracted over multiple scales perform as reliable predictors of deeper reef assemblages. Best models exhibited good to excellent overall performance. The most influential environmental predictors were depth, distance to shore, topographic complexity, slope and curvature, and substrate characteristics. The relative importance of predictors was influenced by assemblage functional characteristics. Assemblage-environment relationships were used to produce probability distribution maps that showed similar distributional patterns for identified assemblages across locations, with high occurrence probabilities linked to complex geomorphological structures. Obtained results help contribute to a consistent baseline understanding of the relationship between seascape structure and mesophotic reef ecosystems in this area. Complex geomorphological structures, including terraces

and paleoshorelines, supported high densities of mesophotic assemblages and could be considered priority habitats for management.

4.1 Introduction

Mesophotic coral ecosystems (MCEs, 30-150 m) and rariphotic habitats (150-300 m) are widespread in tropical and subtropical regions (Pyle & Copus, 2019). These "deeper reefs" host biodiverse communities of interest to conservation (Soares et al., 2020), provide key ecosystem functions and services including food provision, and refuge for some depth-generalist reef species affected by climate change-induced rising sea temperatures and/or shallow-water disturbances (Holstein et al., 2019).

Although deeper reef research is increasing globally, for many tropical regions the distribution and biological data from these habitats is unavailable due to the financial, technological and operational constraints of underwater surveys beyond the depth limits of most airborne sensors and conventional SCUBA diving (> 30-50 m depth) (Woodall et al., 2018). Consequently, the environmental factors shaping deeper reef assemblages remain poorly described for most areas (Turner et al., 2017). This is particularly acute for remote oceanic regions of the Western-Indian Ocean (WIO), which are among the least explored marine areas on Earth and even more so at greater depths (Osuka et al., 2021; Pyle & Copus, 2019). Improving our understanding of the environmental factors that drive deeper reef ecosystems is important for ecosystem-based management approaches aiming to identify seascape features important for ecosystem health and functioning (Bridge et al., 2020; Hinderstein et al., 2010).

Improvements in acoustic remote sensing technology have increased the availability of Digital Bathymetric Models (DBMs) of seabed environments that represent seascape geomorphology as continuous topographic models (Lecours et al., 2015). Terrain metrics are ecologically relevant quantitative derivatives from bathymetric data, such as slope, orientation, topographic complexity, and curvature, that can be used to model the environmental factors driving ecological distributions (Wedding et al., 2011). Indeed, seabed topography is a demonstrated driver of habitat suitability and benthic species

distributions, and terrain derivatives may also act as a proxy for parameters on which detailed data is unavailable (Brown et al., 2011; Wilson et al., 2007).

Geomorphology also influences deeper reef occurrence and distribution through its effects on habitat structure and substrate characteristics and by mediating biotic and abiotic processes. For example, structurally complex habitats may provide a variety of microhabitats that organisms can use for settlement, shelter and feeding (Graham & Nash, 2013; Silva & MacDonald, 2017) and slope, curvature or orientation can mediate hydrodynamic properties of water flow past the reef system influencing disturbance regimes or food availability (Bridge et al., 2011b; Locker et al., 2010; Sterne et al., 2020; Wilson et al., 2007). Substrate characteristics, mediated by site geomorphology, further drive the occurrence and distribution of reefs, as hard substrates provide suitable settlement structure and may support more biodiverse assemblages than mixed or soft substrata (Sherman et al., 2019).

The quantification of seabed structure from bathymetry combined with data from visual surveys of deeper reefs has enabled the application of predictive distribution modelling as a tool to address biogeographical and ecological knowledge gaps (Costa et al., 2015; Guisan et al., 2013). Predictive distribution models that result in maps of expected habitat suitability have become critical tools to inform the design of effective conservation measures (Bridge et al., 2020). Distribution modelling approaches can investigate environmental relationships at the taxon level of interest and apply these to create predictive habitat suitability maps. Previous distribution modelling studies on mesophotic reefs predominantly have a single-species focus, often corresponding to a dominant species or taxa (Costa et al., 2015; Silva & MacDonald, 2017; Sterne et al., 2020; Veazey et al., 2016). Although most prevalent, these efforts might not always be representative, as deeper reefs often comprise diverse benthic communities, including corals, sponges and algae with no single dominant group or taxon (Bridge et al., 2011a; Kahng et al., 2010; Turner et al., 2017; Van Oppen et al., 2005). Assemblage-based predictive models can incorporate multiple species, including low abundance species in a single model (Brown et al., 2011; Ferrier & Guisan, 2006).

Few studies globally study the occurrence of both MCE and rariphotic megabenthos at the assemblage level (e.g. Stefanoudis et al. 2019), and even fewer relate assemblages to local geomorphology. In addition, detailed deeper reef biological occurrence and distribution data are unavailable for many parts of the WIO (Osuka et al., 2021; Pyle & Copus, 2019; Soares et al., 2020). To contribute to filling these knowledge gaps, this study classifies and predictively models the distribution of deeper reef benthic assemblages around remote WIO atolls using digital bathymetric models and underwater video. Specifically, terrain metrics were applied to determine if seabed terrain structure quantified at multiple scales can act as a reliable proxy for predicting deeper reef assemblage distribution. The hypothesis is that the distribution and occurrence of mesophotic assemblages can be adequately explained by combinations of multiscale environmental parameters as assemblages consist of taxa that are likely to respond differently to environmental conditions and at different spatial scales. This hypothesis is addressed by: 1) clustering biological observations to categorize assemblage composition at each site; 2) testing assemblage associations with multiscale terrain metrics and their relative importance in driving assemblage occurrence and distribution; 3) defining habitat preferences for these assemblages based on metric ranges identified, and 4) identifying geomorphological features that may represent priority habitats for conservation by predicting the spatial distribution of assemblages.

4.2 Methods

4.2.1 Study area

Seychelles is an archipelagic state in the Western Indian Ocean. This study focused on four coral atolls: three in the Amirantes island Group: Desroches (DES), St. Joseph (StJ) and Poivre (POI), and one in the Aldabra Group: Aldabra (ALD) (Fig 4.1 a). Biological ground-truthing and multibeam echosounder data were collected at every site (Fig 4.1 b-e) between March and April 2019 during Seychelles First Descent (Woodall & Rivers, 2019).

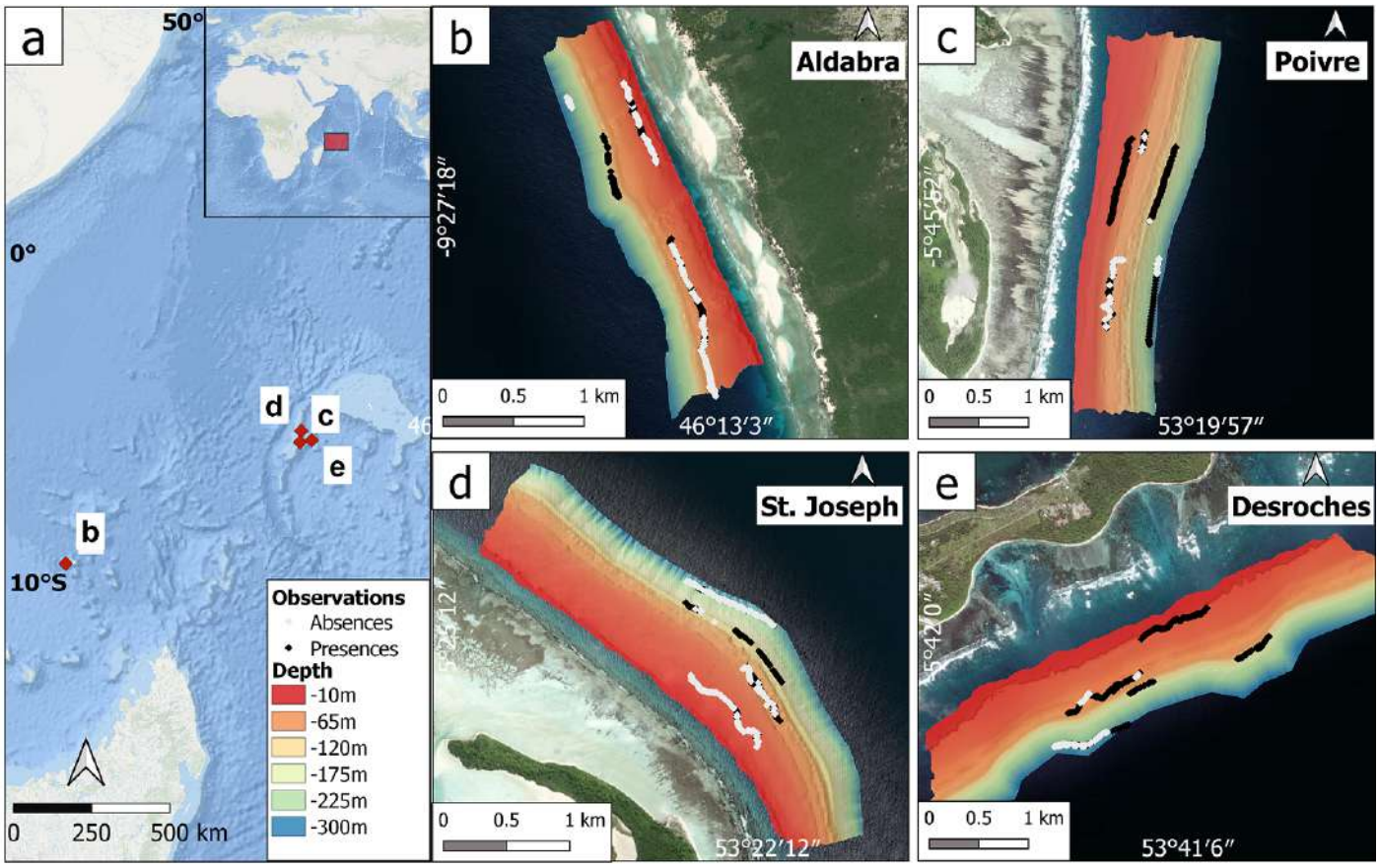


Figure 4.1: Research locations within the Seychelles archipelago (a) and bathymetry and submersible video transect tracks at each study site (b-e). White and black dots indicate absences and presences of deeper reef assemblages respectively. Area surveyed at each site was approximately 2km^2

4.2.2 Biological data collection and preparation

At each site, three replicate 250 m long video transects were collected at four target depths(30 m, 60 m, 120 m and 250 m) using stereo-sets of video cameras (Paralenz DiveCamera+) mounted on a submersible (Triton 1000/2). Photo frames were extracted every 30 seconds from video data, and each photo frame was linked to a geographical position (latitude, longitude and depth) corresponding to submersible location obtained using a Kongsberg HiPaP 501 (+/- 2 m accuracy). The best quality photograph of each stereopair was then selected for biological and substrate data annotation by scientists at the Nekton Foundation. Photo frames were excluded from the analysis if no USBL positioning data were available, if photo quality was inadequate for video annotation (low light, blurry, obstructed) and when submersible distance from the seabed was too

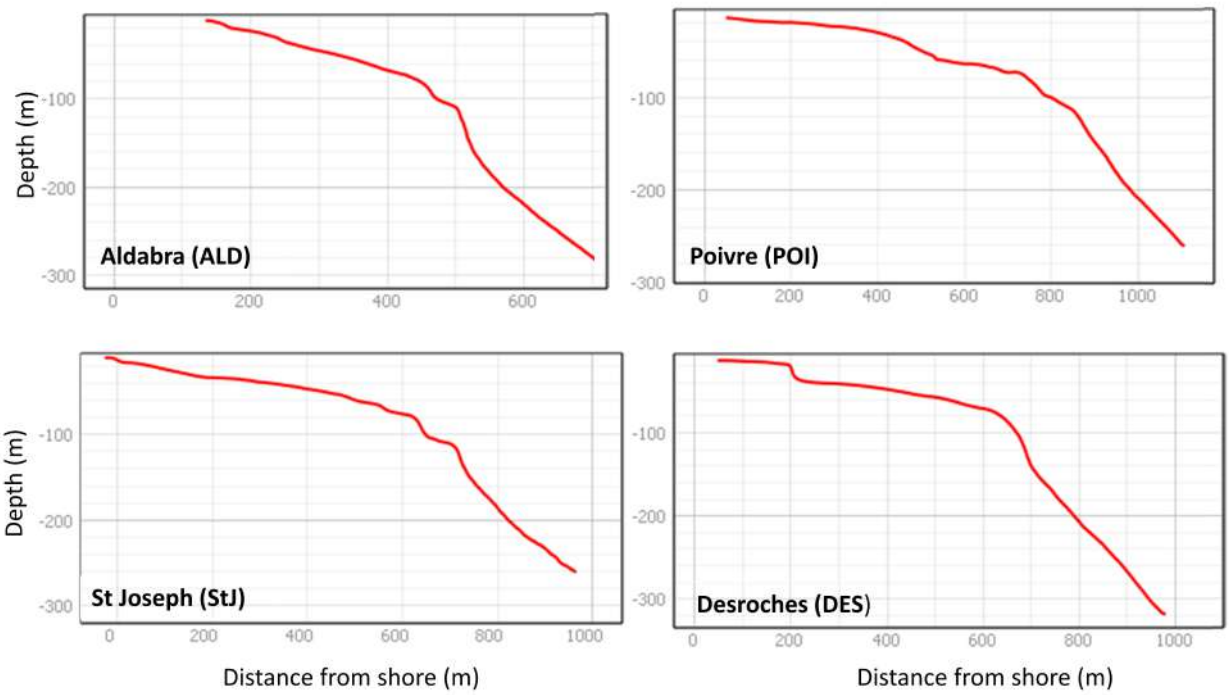


Figure 4.2: Geomorphological profiles (0-300 m) per site

great to allow positive identification of benthos (=photos covering an area > 8m^2).

With the image analysis software TransectMeasure from SeaGIS (Seager, 2014), retained photo frames were annotated using twenty random points per m^2 classified as either a substrate type (i.e. sand and mud, coral rubble, pebbles, boulders, bedrock) or a living organism. Sessile megabenthos was placed into morphotypes (=morphologically similar specimens) identified to the lowest possible taxonomic level, which most commonly was genus or family (Fassbender et al., 2021) as identification to species level would require microscopic examination in many cases (Stefanoudis et al., 2019). Interpreter error was minimised through cross-checking by researchers. Per photo frame, substrate classifications were averaged and merged according to the majority rule (> 50% of points) to hard (bedrock, rubble, boulders, cobbles - class 1), mixed (when substrate types occurred in equal proportions, class 2) or soft (mud, sand, sediment - class 3) substrate. Using this method, 350-500 annotated photographs were extracted per site. When no organisms were visible in the photo an absence was recorded. Per site, 350-500 data points providing information on substrate type and organisms present were extracted using this method. The total

surface area annotated averaged 749 m^2 per survey site (Aldabra: 931 m^2, St Joseph: 595 m^2, Poivre: 628 m^2 and Desroches: 843 m^2).

Hierarchical agglomerative clustering based on Bray-Curtis dissimilarity and Ward's minimum variance method was conducted to identify clusters of co-occurring taxonomic groups at each site, using the package vegan (Oksanen et al., 2018) in R version 3.5.1 (R Core Team 2018). Each photo was assigned an assemblage class, as defined by the clustering analysis. The optimum number of clusters for each site was determined by maximizing Dunn's index, an internal evaluation scheme that maximises the separation between clusters and minimises the variance within clusters (Dunn, 1973). Clustering results were visualized using non-metric multidimensional scaling (nMDS) plots and PERMANOVA was used to confirm their statistical significance ($p < 0.05$). Taxa could be assigned to multiple assemblage clusters, and the contribution of recorded taxa to clusters per site was assessed using permutational Dufrene-Legendre indicator species analysis (Dufrene & Legendre, 1997) in R package indicspecies (de Caceres, 2009). The indicator value index assigns taxa a p-value as a function of their relative abundance and frequency of occurrence in different groups, where $p \geq 0.05$ indicates that taxa are characteristic of that cluster and a $p \leq 0.05$ indicates taxa do not have a significant cluster affiliation.

4.2.3 Environmental predictors

To understand the geomorphological structure of each site, bathymetry and acoustic backscatter data were collected at each site over an average area of $2km^2$ between 0 and 300 m depth, using a Teledyne Reson Extended range SeaBat T50-P multibeam echosounder and the Teledyne PDS acquisition software. Qimera (QPS) software was used to process and grid the bathymetric data. Backscatter data were processed using the FMGeocoderToolbox (Fledermaus™ software, QPS). Positioning data was collected using an Applanix POS MV system and processed using Applanix POSPac. Despite post-processing, bathymetry data contained some small artefacts at Desroches and Poivre in areas < 70 m and backscatter data was oversaturated in areas beyond 150 m

depth at most sites (Appendix C.3). As oversaturation was only a problem for these deeper depths, backscatter was nevertheless included as predictor variable.

Ecologically relevant terrain derivatives were extracted in ArcMap 10.6 using Benthic Terrain Modeller (BTM) (Walbridge et al., 2018) and in R using the raster (Hijmans, 2017) and spatialEcology (Evans, 2017) packages. Parameters derived from bathymetry data were chosen to represent four broad geomorphological classes: slope, orientation, curvature and terrain variability (Wilson et al., 2007). Parameters describing substrate type and geographic position were also quantified (Table 4.1). Although correlation between assemblage occurrence and sampling depth is expected as a result of the sampling design, depth was included as a continuous predictor to enable meaningful spatial predictions outside of sampling depths. Where variables exhibited high collinearity (Pearson correlation $> |0.7|$), the variable allowing for more intuitive ecological interpretation was retained (Dormann et al., 2013), whilst ensuring the four broad classes of metrics describing terrain structure were represented. The substrate classes identified in the annotation process (soft, mixed, hard) were used as ground-truthing for a random forest classification (Breiman, 2001) using the non-collinear predictors excluding backscatter.

To investigate the influence of spatial scale on the relationships between terrain morphology and assemblage structure, terrain derivatives were extracted from bathymetry resampled to three spatial resolutions (2 m, 10 m, 25 m). The highest gridding resolution of bathymetry data determined the finest spatial scale (2 m). The appropriate broad scale was determined using Dragut's Estimation of Scale Parameter (ESP) Tool (Drăguţ et al., 2010), where a decline in Rate of Change of Local Variance (ROC-LV) curves was observed at a resolution of 25 m. Derivatives were also calculated at 10 m resolution to account for intermediate-scale effects and following resolutions used in other mesophotic reef studies (Costa et al., 2015; Sterne et al., 2020). Although variables at multiple scales exhibited collinearity, these were retained to account for possible multiscale effects of predictors on assemblage occurrence and distribution. Machine learning algorithms used in this study are less sensitive to collinearity and

can be parameterized to avoid overfitting whilst dealing with several variables and interactions (Costa et al., 2015; Misiuk et al., 2018).

A data layer representing substrate class was included to provide more meaningful data on substrate type than the backscatter data alone. The substrate classes identified in the annotation process (soft, mixed, hard) were used as ground-truthing for a random forest classification (Breiman, 2001) using the non-collinear predictors to obtain this data layer. The final set of predictor variables can be found in Table 4.1.

Table 4.1: Predictor variables explored and retained to quantify seascape structure. The table indicates their ecological relevance, method of extraction and spatial scales retained for analysis

	Parameter	Unit	Ecological Relevance	Scale (m)	Calculated in	Retained?
Depth	Water Depth	Meters	Relates to several environmental parameters including light penetration, temperature and productivity	2x2 m, 10x10 m, 25x25 m	Bathymetry	Yes
Slope	Slope	Degrees	Measures elevational change, which is a proxy for substrate, local hydrodynamic regime and sedimentation	2x2 m, 10x10 m, 25x25 m	R Raster	Yes
Aspect	Orientation (measured as eastness (sinasp) and northness(cosasp))	Radians	Reflects the orientation of the seabed, which is a proxy for current exposure	2x2 m, 10x10 m, 25x25 m	R Raster	Yes
Curvature and relative position	Total curvature (curv)	Measured in 1/100th of a z-unit (m) in ArcGIS	Second derivative of bathymetric surface, Measures the convexity/concavity of the seascape, which gives information on the orientation and relative elevation of the surface	2x2 m, 10x10 m, 25x25 m	ArcGIS 3D Analyst	Yes
	Plan curvature (curvature_pl)		Plan curvature is the second derivative only evaluated perpendicular to slope (horizontal plane), which influences flow convergence and divergence	2x2 m, 10x10 m, 25x25 m	ArcGIS 3D Analyst	Yes
	Profile curvature (curvature_pr)		Profile curvature is the second derivative only evaluated parallel to the slope (vertical plane), which affects flow speed and resulting erosion and deposition	2x2 m, 10x10 m, 25x25 m	ArcGIS 3D Analyst	Yes
	BPI Bathymetric Position Indexs	Mean elevation value in m within analysis neighbourhood	Indicates whether an area is part of a positive or negative feature of the surrounding terrain, which is a proxy for exposure or shelter opportunities	2x2 m, 10x10 m, 25x25 m	R spatialEco	No, collinear with curvature
Terrain variability	Arc-chord Rugosity (ACrug)	Unitless ratio	The ratio of surface area to planar area of best fit, which decouples rugosity from slope, unlike the normal rugosity calculation	2x2 m, 10x10 m, 25x25 m	BTM (ArcMap 10.6)	Yes

	VRM vector ruggedness measure	Dimensionless value ranging from 0 (no variation) to 1 (high variation)	Measures the variation in the three-dimensional orientation of grid cells within a neighbourhood as proxy for habitat heterogeneity	2x2 m, 10x10 m, 25x25 m	R spatialEco	No, collinear with arc-chord rugosity and slope of slope
	TRI Terrain Ruggedness Index	Meters of elevation difference between grid cells	Reflects local variation in seabed terrain, associated with changes in habitat complexity	2x2 m, 10x10 m, 25x25 m	R spatialEco	No, collinear with rugosity and slope
	Slope of slope	Degrees of degrees	Measures the change of the slope gradient as measure of terrain variability	2x2 m, 10x10 m, 25x25 m	R Raster	Yes
Substrate	Backscatter (BS)	dB	Measure of the seabed reflectivity, which is a proxy for substrate type	2x2 m, 10x10 m, 25x25 m	NA	Yes
	Substrate type (created using random forest classification of other terrain variables)	Classified values	Classified as hard (class 1), mixed (class 2) or soft (class 3) . Substrate characteristics affect organism settlement and colonization	2x2 m	R raster, caret	Yes
Geographic	Distance to shore	m	Geographic proxy for variables relevant for deeper reef recruitment and growth, including current regime and turbidity influencing light availability, and sea surface temperature	2x2 m	ArcMap 10.6	Yes. Although distance to shore was expected to be coupled with depth, Pearson correlation was lower than $\|0.7\|$

4.2.4 Model selection, building and evaluation

Random forests (RF) (Breiman, 2001) and boosted regression trees (BRT) (Friedman, 2001) were used to generate spatial predictive models. RFs and BRTs are examples of ensemble decision trees, non-parametric approaches without distribution assumptions that can fit complex responses, cope with interacting predictor variables and filter out irrelevant predictors (Elith et al., 2008). Where the RF algorithm creates decision trees by fitting individual trees to each replicate of a bootstrap sample of a training set and a subsample of the explanatory variables, BRTs combine this approach with boosting methods by building many decision trees in which every tree learns from the previous. RFs and BRTs have been used for a variety of applications in marine ecology, including modelling the distribution of species and assemblages, both of benthos (Du Preez et al., 2016; González-Irusta et al., 2015; Robert et al., 2016) and fish (Leathwick et al., 2006; Pittman & Brown, 2011; Pittman et al., 2009), habitat mapping (Porskamp et al., 2018), seabed substrate mapping (Herkül et al., 2017; Misiuk et al., 2018), and MPA planning (Leathwick et al., 2008).

R packages randomForest (Liaw & Wiener, 2002) for RF models and gbm (Ridgeway, 2017) for BRT models were implemented through the package caretEnsemble (Deane-Mayer & Knowles, 2016). The model building process was identical for each assemblage cluster and site. A presence-absence dataset was created for each assemblage, where observations assigned to that assemblage through clustering were scored as presences (Table 4.2). The values of predictor variables were subsequently extracted from the raster cell corresponding to the geographic x,y,z location of each photo frame. The number of trees and number of variables available for splitting at each node (mtry) were optimised in RF models, and the number of trees, interaction depth (complexity) and shrinkage (learning rate) in BRT models. The best model was selected using the smallest value for the mean absolute error (MAE). The evaluation dataset was obtained by structured sub-sampling of the training data set during the 10-fold cross-validation process. A performance assessment was conducted by running ten resamples of the produced model.

Evaluated for each model were: 1) model performance in a) discrimination capacity, using the area under the curve of the receiver operating characteristic (AUC-ROC), where a value of 0.9-1 indicates excellent performance, a value of 0.7-0.9 good performance and a value of 0.5 a performance no better than that expected by chance; b) reliability, using the mean absolute error (MAE) which ranges from 0 to 1, with 0 corresponding to a model that is a perfect output predictor; c) spatial autocorrelation in model residuals, using Moran's I and d) visual accuracy; 2) the contribution of predictors to each model using variable importance analysis; 3) habitat preferences for each assemblage with partial dependence plots (Milborrow, 2020) and density plots (Bowman & Azzalim, 2018) and 4) predicted assemblage occurrence and distribution over the entire site.

4.3 Results

4.3.1 Cluster composition

Cluster analysis resulted in four assemblage clusters for each site (Fig. 4.4, Table 4.2, Table C.2.1 in Appendix C.2), which despite some overlap between assemblages 1-3 (Fig 4.3), all differed significantly in composition (PERMANOVA $p < 0.001$, Table C.2.2 in Appendix C.2).

Indicator species analysis performed on these assemblage clusters demonstrated that, although the exact taxa composition of each assemblage cluster differed per site, they corresponded to similar biological zones linked to sampling depth (Fig. 4.4, Table 4.2). Assemblage 1 (30 m-60 m, Fig. 4.4 a) contained scleractinians and zooxanthellate octocoral, macroalgae and sponges. Assemblage 2 (60 m, Fig. 4.4 b) is dominated by azooxanthellate octocoral with diverse morphologies, scleractinians showing depth adaptations (e.g. dominance of plating morphologies that enhance monodirectional light absorption), and some antipatharians. Assemblage 3 (120 m, Fig. 4.4 c) consisted mainly of azooxanthellate octocoral fans and encrusting organisms, most notably crustose coralline algae (CCA) and Porifera. Reef-building species were absent from assemblage 4 (250 m, Fig. 4.4 d), which consisted of sea urchins

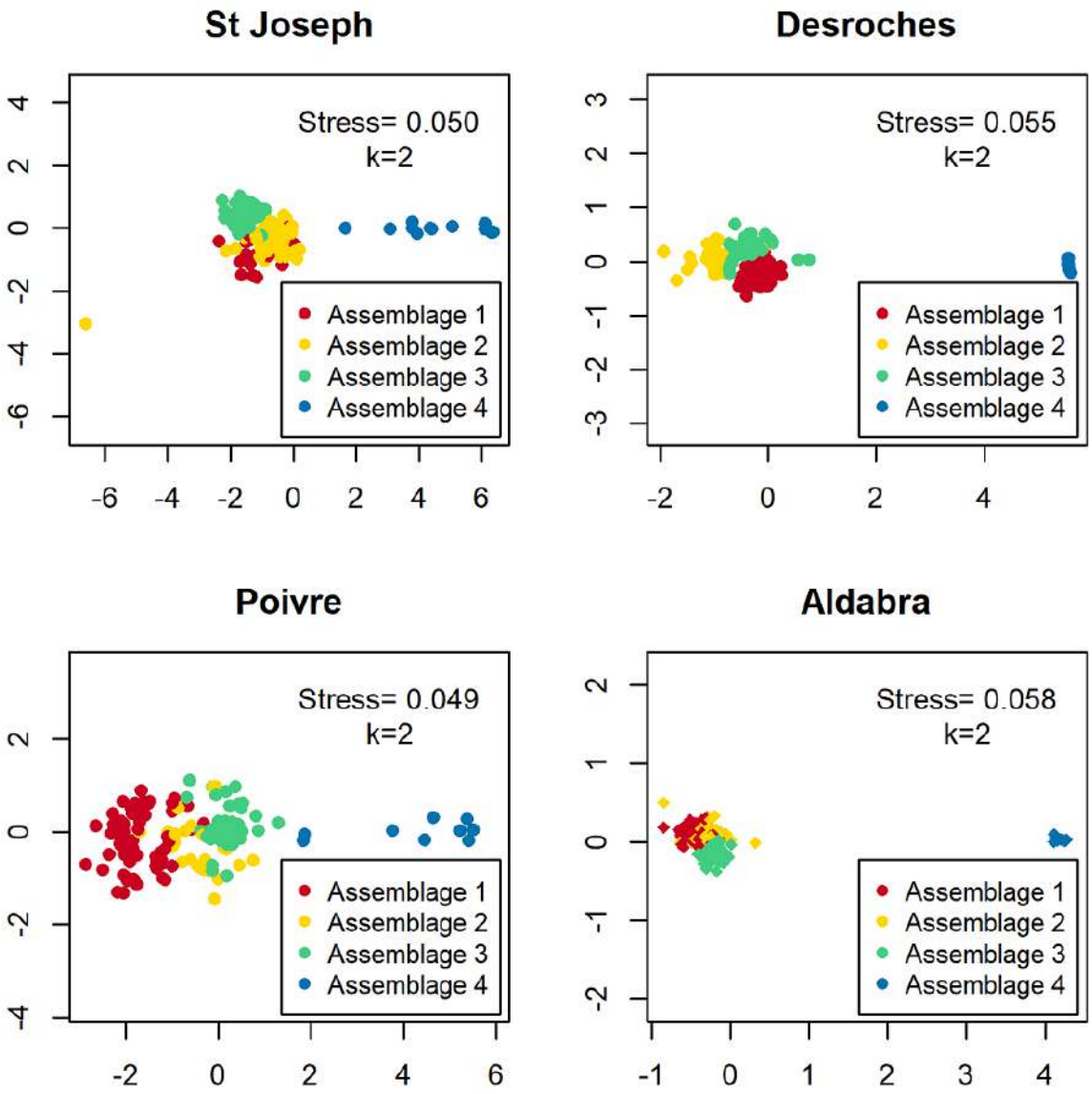


Figure 4.3: nMDS plots visualising the dissimilarity between observations from different assemblages

and sea stars and occasionally hydrocorals (Stylasteridae). Indicator species analysis also revealed generalist taxa that occurred across multiple assemblage clusters, most notably Demospongiae sp. 2, *Hydrozoa* spp. and Corallinales spp., however, it is worth noting that these are coarse taxonomic identifications and hence include several species (Fassbender et al., 2021).

Table 4.2: Taxa significantly ($p < 0.05$) associated with each cluster per site, ordered by indicator value. Taxa are described in Fassbender et al. (2021).

Assemblage	St Joseph	Desroches	Poivre	Aldabra
30-60 m: Scleractinia, Alcyonaceae, Chlorophyta, Demospongiae	*Porites* spp., *Halimeda* spp., *Favites* spp. *Dipsastrea* spp., *Spheciospongia* sp. 1, *Echinophyllia* spp., *Leptoseris* spp., *Stylissa carteri*, *Sinularia* spp.	*Halimeda* spp., *Porites* spp., *Pachyserus* spp., *Stylissa carteri*, *Fungiidae* sp. 2, *Favites* spp., spp., *Fungiidae* sp. 1, *Lobophytum* spp., *Montipora* spp., *Acropora* spp., *Goniastrea* spp.	*Acropora* spp., *Halimeda* spp., *Fungia* spp., *Porites* spp., *Microdictyon* spp., *Fungiidae* sp. 1, *Haliclona* sp. 2, *Udotea* spp., *Sarcophyton* spp.	*Theonella* spp., *Spheciospongia* sp. 1, *Clathria* sp. 1, *Stylissa carteri*, *Porites* spp., *Lobophyllia* spp., *Montipora* spp., *Favites* spp., *Pachyseris* spp.
60 m: Alcyonaceae, Scleractinia, Antipatharia, Demospongiae	*Ellisella* spp., *Dichotella* spp., *Hydrozoa* spp., *Cupressopathes* spp, *Plexauridae* sp. 8	Plexauridae sp. 14, Plexauridae sp. 9, *Ulva* spp., *Viminella/Junceella* spp., Alcyonaceae spp., Plexauridae sp. 8, *Nicella* spp., *Solenocaulon* spp., *Ellisella* spp., *Dendronephthya* sp. 1, *Annella* spp.	*Ellisellidae* sp. 1, *Demospongiae* sp. 3, *Antipatharia* spp., *Ellisella* sp. 1, *Clathria* sp. 1, *Myriopathes* spp.	*Iotrochota nigra*, *Ellisella* spp., *Speciospongia* sp. 2, *Solenocaulon* spp., *Haliclona* sp. 2, Plexauridae sp. 3, *Tetilla* sp. 1
120 m: Rhodophyta, Demospongiae, Antipatharia, Alcyonaceae	*Oceanapia* spp., *Demospongiae* sp. 1, Plexauridae sp. 2, *Tetilla* sp. 1, *Corallinales* spp., *Alcyonaceae* spp., *Ophidiasteridae/ Echinasteridae* spp.	*Heteronardoa diamantinae*, Plexauridae sp. 2, *Oceanapia* spp., Hydrozoa spp., *Tetilla* sp.1	Demospongiae sp. 1, *Tetilla* sp.1, Ellisellidae sp. 1, *Viminella/Junceella* spp., Plexauridae sp.2, *Oceanapia* spp.	*Corallistes* spp., *Litophyton* spp., *Viminella/Junceella* spp., *Nicella* spp., *Pachastrella* spp., *Plexauridae* sp.2, *Plexauridae* sp.6, *Astrogorgia* spp., *Cidaroida* sp.1
250 m: Echinoidea, Hydrozoa, Anthozoa	*Clypeaster* spp., *Stylasteridae* sp. 1, *Stylopathes* spp., *Mycropyga* spp.	*Clypeaster* spp., *Cidaroida* sp. 1, *Micropyga* spp.	*Clypeaster* spp., *Cidaroida* sp. 1, Decapoda spp., *Stylopathes* spp.	Actiniaria sp.1, *Paguroidea* spp., Actiniaria sp.2, *Stylasteridae* sp.2, Decapoda spp.
Indicator taxa associated with multiple clusters:	*Viminella Junceella* spp. (1+2), *Annella* spp. (1+2), Demospongiae sp. 2 (1+2)	Demospongiae sp. 2 (1+2+3), Corallinales spp. (1+3)	*Porites* spp. (1+2), Demospongiae sp. 2 (1+2+3), Corallinales spp. (2+3)	Demospongiae sp. 2 (1+2+3), Hydrozoa spp. (2+3), Corallinales spp. (2+3)

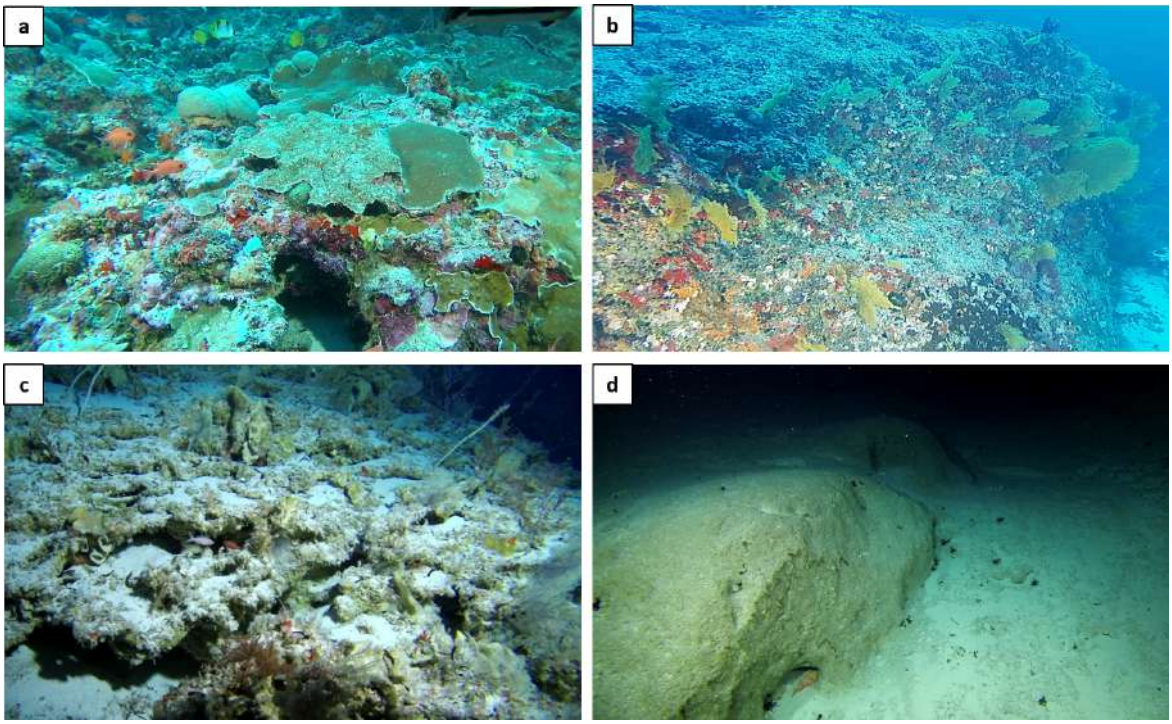


Figure 4.4: Representative examples of assemblage types, where a, b, c and d visualise examples of assemblage 1 (30 m-60 m), 2 (60 m), 3 (120 m) and 4 (250 m) respectively at Aldabra.

4.3.2 Model performance

All models showed good to excellent performance, with some site and assemblage-specific variation (Table C.3.1 in Appendix C.3). With ROC-AUC values between 0.86 and 0.99 for RF (mean 0.95, sd 0.021) and 0.86 and 0.99 for BRT models (mean 0.94, sd 0.024), discrimination capacity was good to excellent for all models (Fig 4.5a, c), and comparable between algorithms. Discrimination capacity was higher for assemblage 3 than other assemblages, with some site-specific variation without clear pattern. Like discrimination capacity, model reliability (Fig 4.5 b,d) was good to excellent, with mean MAE ranging from 1.3% to 18.4% for RF (mean 9.2%, sd 1.8%) and from 1.6% to 18.2% for BRT models (mean 9.8%, sd 1.4%), comparable between algorithms. Model reliability was again high for assemblage 3 (mean MAE $< 6\%$) and reduced for assemblages 1 and 2 (mean MAE up to 18%) with some site-specific variation. Although there was no significant residual spatial autocorrelation in BRT or RF models for assemblages 1, 2 and 3 calculated using Moran's I ($p > 0.05$), there

was for assemblage 4 ($p < 0.05$) (Table C.3.1 in Appendix C.3).

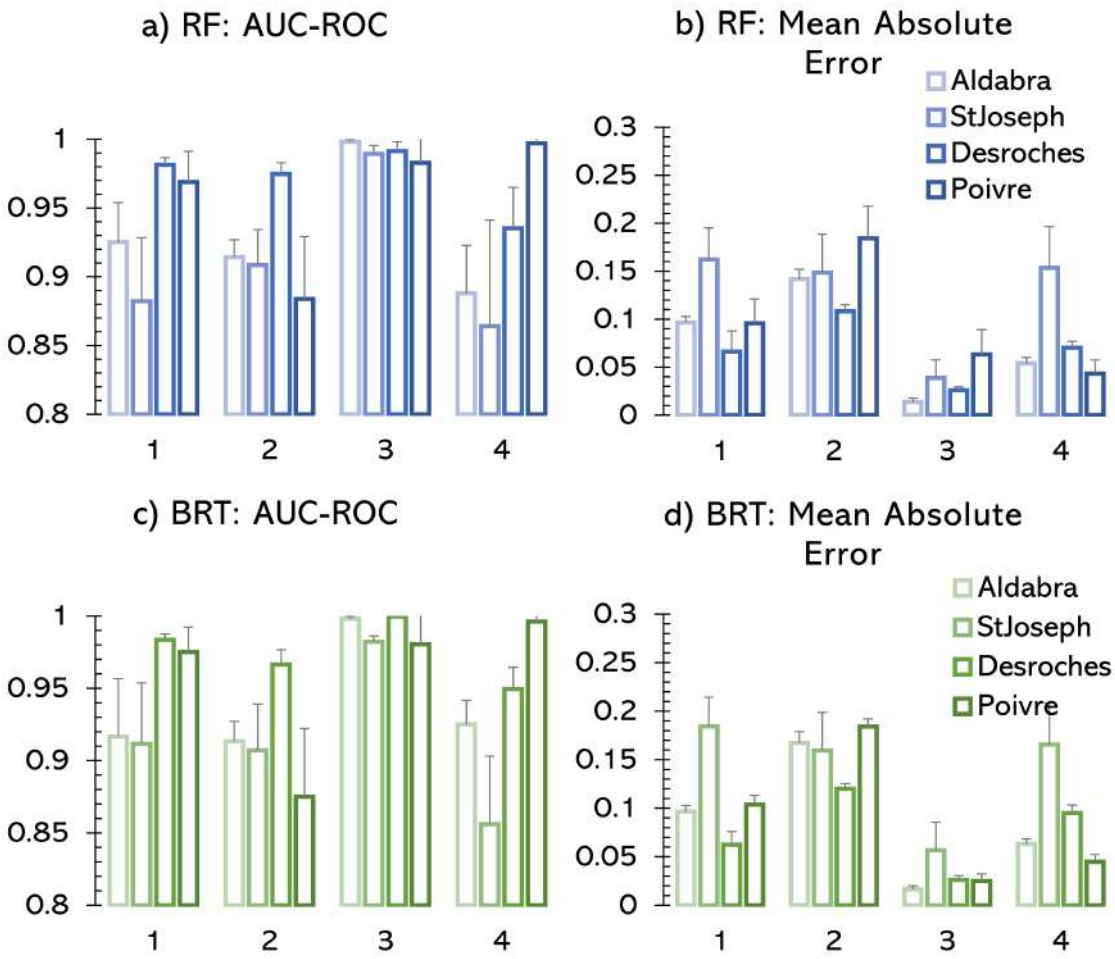


Figure 4.5: Performance statistics for models. Discrimination capacity was measured as AUC-ROC for RF models (a) and BRT models (c) per assemblage. Accuracy was measured as Mean Absolute Error for RF (b) and BRT (d). Standard errors were calculated as a function of 10 model iterations.

4.3.3 Predictor contributions to distribution models

Overall, the main determinants of assemblage occurrence (measured by variable importance) were depth, distance to shore, arc-chord (AC) rugosity, curvature, slope and backscatter. Predictor variables calculated at 25 m and 10 m resolutions contributed more to the model than predictors calculated at the 2 m resolution, but were correlated. Primary predictors were consistent between model algorithms and geographical location. Variable importances showed that RF (Fig 4.6 a-d) models were often characterised by

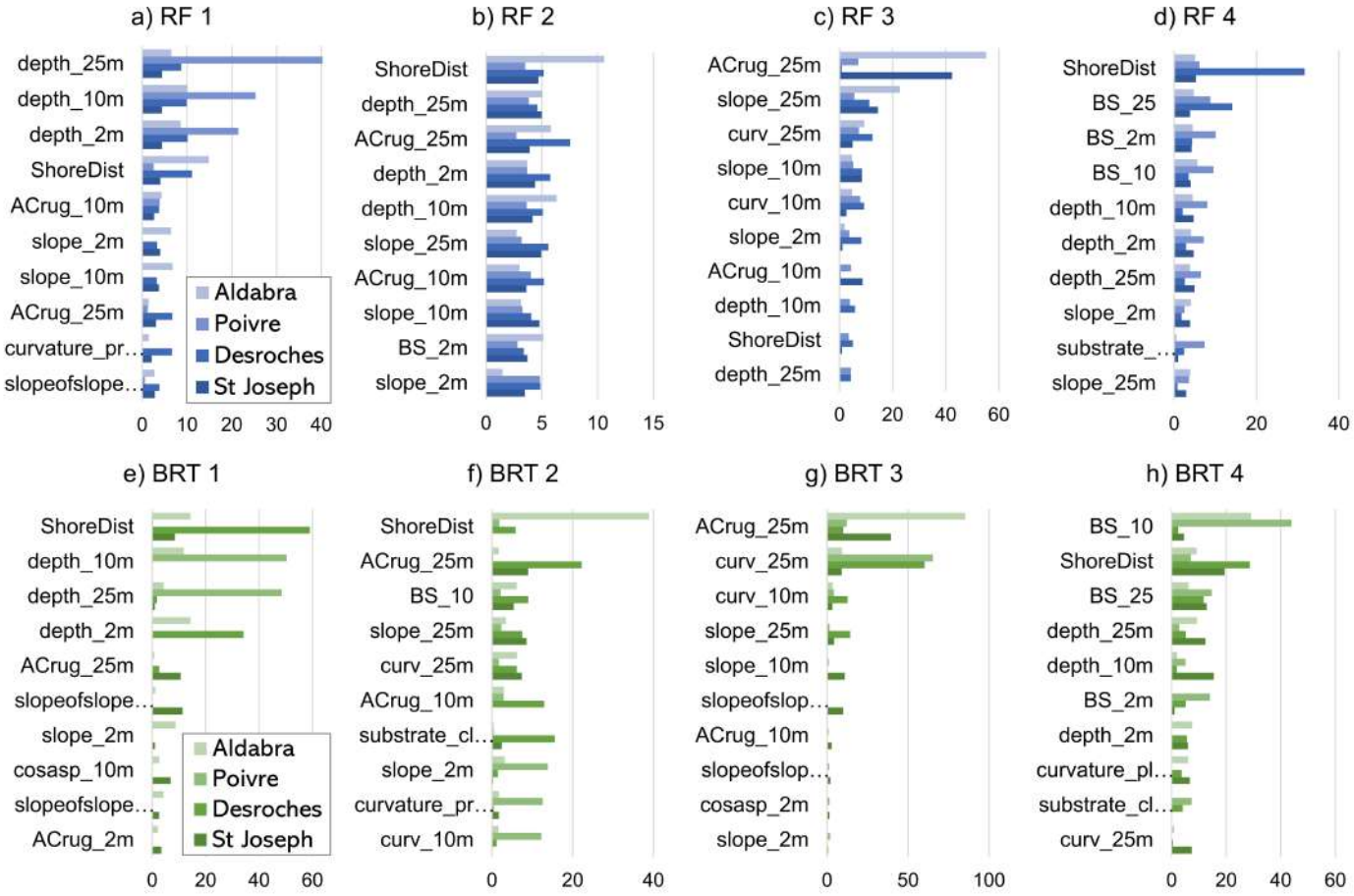


Figure 4.6: Relative contribution of the ten main predictors per assemblage across sites, assessed for Random Forests (a-d) and Boosted Regression Trees (e-h). Variable importance was calculated as the mean decrease in node impurity and standardised as a percentage

smaller contributions of multiple predictors extracted at different scales, whereas the relative contribution of individual predictors was greater for BRT models (Fig 4.6 e-h) which filtered out predictors with low model contributions. The relative importance of these main predictors also varied with assemblage type.

The most important predictors of assemblage 1 were depth, distance to shore and terrain complexity (AC rugosity). Predictors associated with assemblage 2 also included depth, distance to shore, and terrain complexity (AC rugosity), with slope and curvature important in BRT models. A smaller set of predictors contributed to the models of assemblage 3 and included curvature, terrain complexity (AC rugosity) and slope. Finally, depth, distance to shore and backscatter, which was oversaturated

at these depths (Appendix C.3), contributed most to models of assemblage 4.

4.3.4 Predicted MCE habitat suitability

Deeper reef assemblage habitat preferences were derived from partial dependence plots (Fig. C.4.1 to C.4.16 in Appendix C.4) and density plots (Fig. 4.7 and Fig. C.5.1 to C.5.3 in Appendix C.5). Partial dependence plots revealed that many key predictor variables had a non-linear relationship with model predictions. They also showed that key predictors (apart from depth and slope) exhibited variable multiscale effects on model predictions, with the effects of predictors extracted at fine-scale (2 m) often different from the effects of broad-scale (10 m and 25 m) predictors. Density plots were constructed using six broad-scale predictors that consistently contributed most across assemblages and models, and revealed that assemblages were segregated by depth and distance to shore but mediated by terrain drivers important for individual assemblages.

Probability maps produced with the best performing models showed potential spatial distributions of each assemblage per site (Fig. 4.8 and Fig. C.6.1 to C.6.3 in Appendix C.6) and linked potential habitat characteristics identified using the partial dependence plots and density plots to geomorphological features. Assemblages 1 and 2 were distributed over the insular shelf and exhibit high probabilities on elevated complex terrain as reef crests (Aldabra, Desroches), rocky ridges (Poivre) or terraces (St. Joseph). High probability densities of assemblage 1 are found closest to shore on either flat to gently sloping areas of low rugosity (AC rug < 1.01) on a mixed substrate (St. Joseph, Poivre, Fig. 4.7 a, b, c) or rugose (AC rug > 1.02) hard terrain such as ridges (Aldabra, Desroches). Across sites, high probability densities of assemblage 2 are linked to water depths extending to 75 m on slightly sloping (slope $< 30^{o}$) or slightly curved terrain of hard to mixed substrate types (Fig. 4.7 a, d, e). Assemblage 3 was environmentally distinct from other assemblages, with high probability densities on steeply sloping (slope $> 40^{o}$), highly positively (St. Joseph, Poivre, Aldabra, Fig. 4.7 c, d, e) or negatively (Desroches) curved and rugose (AC rug > 1.02) terrain beyond depths of 100 m. These correspond to highly complex and sloping rocky ridges, including paleo-shorelines. Probability distributions for assemblage 4 were located on

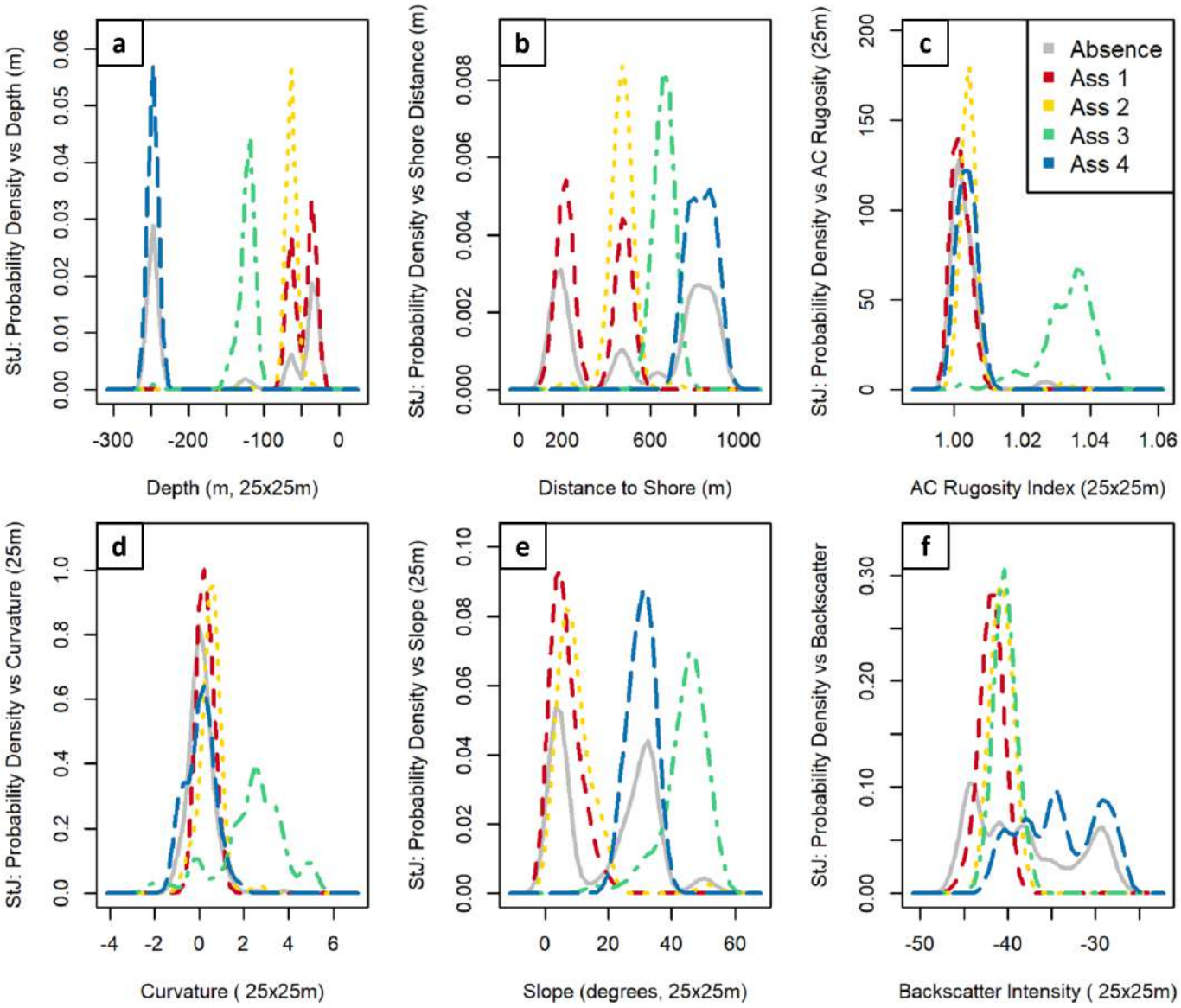


Figure 4.7: Density plots of assemblage response to the consistently highest contributing predictors (depth (a), distance to shore (b), rugosity (c), curvature (d), slope (e) and backscatter (f)) extracted at the broadest resolution (25 m) at St Joseph. Density plots for Aldabra, Poivre and Desroches can be found in Appendix C.5

insular slopes and separated from those for assemblage 1, 2 and 3 (Fig. 4.7 a, b, e), and generally were higher in low rugose areas beyond 200 m furthest from shore on soft to mixed substrate (substrate class = 1 or substrate class = 2) consisting of sand or bedrock covered with sand and related to high backscatter intensities. However, the occurrence of assemblage 4 was environmentally not distinct from biological absences, as high probabilities of assemblage absences were found in similar environmental

conditions as occurrences of assemblage 4 (Fig. 4.7 a, b, e, f). Regardless of site and model type used, spatial predictions of assemblage 4 were unreliable and strongly linked to oversaturated backscatter data beyond 150 m depth, particularly pronounced at Poivre and Desroches where assemblage 4 is predicted to occur in segregated sections that correspond to inflated values of backscatter intensity.

RF and BRT models show similar results in predicted assemblage locations but differ in the predicted extent and probability level. Probability distributions from BRT models appeared more sensitive to data artefacts or input data uncertainty. This was demonstrated in the probability maps of assemblage 1 at Desroches and Poivre (Appendix C.6) where bathymetric data < 70 m suffered from some artefacts.

4.4 Discussion

Mesophotic and rariphotic reef ecosystems are increasingly recognised as important biodiversity hotspots in the global tropics, but major knowledge gaps remain on the environmental factors that interact to influence assemblage structure, occurrence and resulting geographical distributions (Turner et al., 2019). By using an assemblage-level analysis this study showed that deeper reefs consist of depth-separated assemblages that exhibit distinct responses to terrain variables, and predicted extensive and previously unreported potential deeper reef habitat at all study locations.

4.4.1 Drivers and distribution of mesophotic assemblages

Across MCE assemblages, predicted distributions were strongly segregated by depth and distance to shore, both proxies of decreasing temperature and light penetration (Kleypas et al., 2015) that strongly influence MCE occurrence (Tamir et al., 2019; Turner et al., 2017). Moreover, substrate characteristics also drive and limit deeper reef occurrence: hard substrates provide settlement opportunities and may support more biodiverse deeper reef assemblages than mixed or soft substrata (Sherman et al., 2019). As expected, the occurrence of individual assemblages was related to interacting effects of multiple predictor variables and appear related to their functional characteristics.

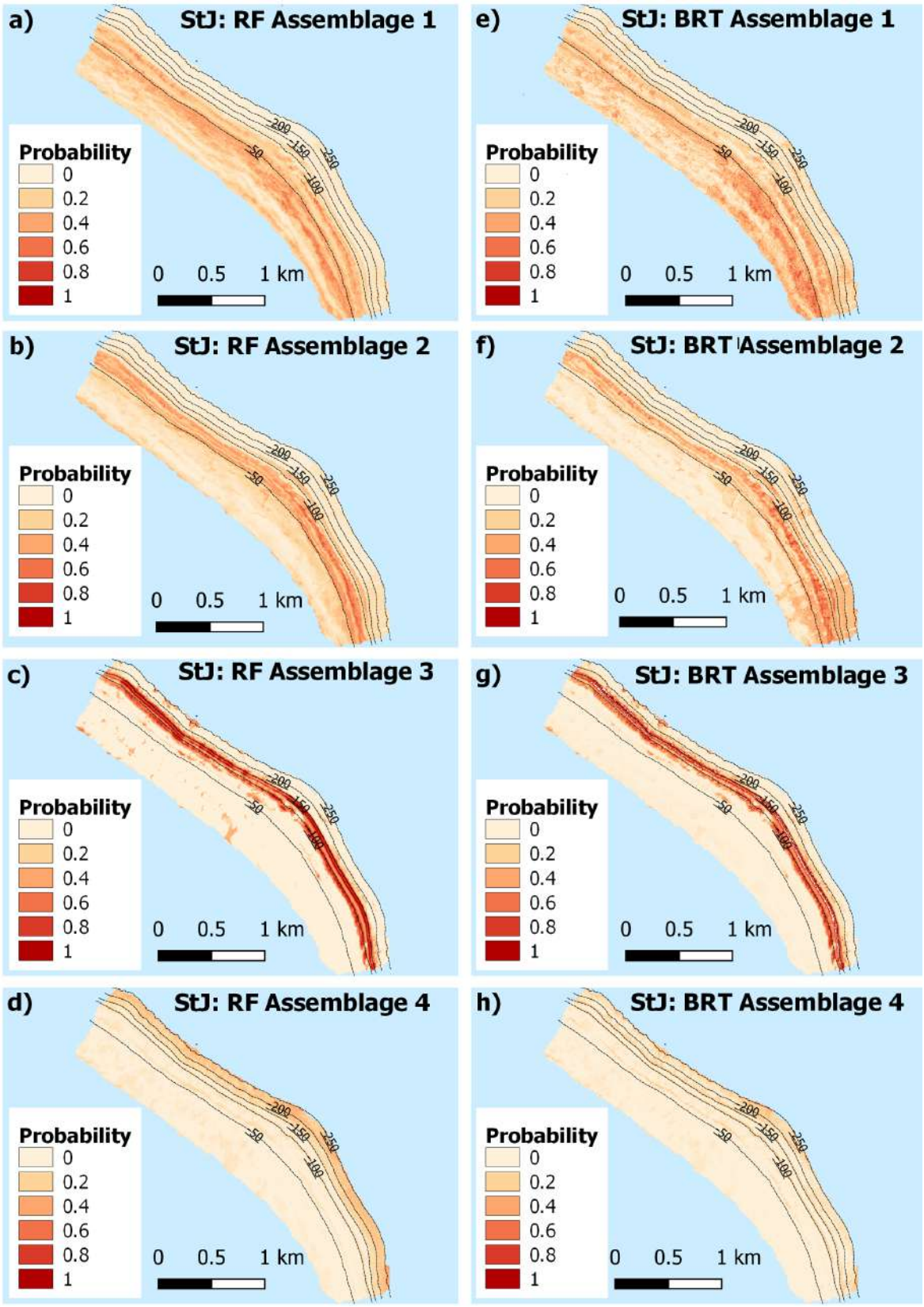


Figure 4.8: Spatial predictions for deeper reef assemblages at St. Joseph produced using Random Forests (a-d) and Boosted Regression Trees (e-h) with depth contours at 50 m intervals. Predictive maps for other sites (Aldabra, Desroches, Poivre) are available in Appendix C.6

Assemblage 1, composed of obligate zooxanthellate reef-building taxa (Table 4.2), is found in well-lit reefs between 30-60 m, which tend to be closest to island coastlines. Its occurrence was linked to complex terrain and hard substrate, but these values may be amplified as biogenic reef species found in assemblage 1 further contribute to the availability of complex terrain and hard substrate. Assemblage 2 contained both zooxanthellate and azooxanthellate species and is therefore in part associated with depths where sufficient light penetrates to enable photosynthesis. Assemblage 2 was also associated with slope and curvature which mediate hydrodynamic properties of water flow past the reef system, influencing food availability for heterotrophic suspension-feeding organisms (Bridge et al., 2011b; Locker et al., 2010; Sterne et al., 2020). Increased slope values may also shield taxa characterised by flattened morphologies found in assemblage 2 from heavy sedimentation (Kahng et al., 2010; Ohlhorst & Liddell, 1988). Assemblage 3 consisted of encrusting morphotypes and azooxanthellate octocorals, and high habitat complexity strongly predicted its occurrence, mirroring results found in previous studies on mesophotic octocorals (Silva and MacDonald 2017). Structurally complex habitats may provide a variety of microhabitats that organisms can use for shelter and feeding, create additional settlement space for encrusting organisms, and finally induce increased current flow that may bring food particles necessary for suspension-feeding octocorals (Pygas et al., 2020). The steep slopes and walls at 120 m depth, where assemblage 3 was also found, direct downward sediment transport (Kahng et al., 2010). In this context, locally elevated features, measured by terrain curvature, might prevent communities being covered by sediment falls (Sherman et al., 2019). Assemblage 4 was found beyond 200 m depth, but it proved challenging to define habitat conditions. Megabenthos characterizing these assemblages occur on patches of hard substrate interspersed among soft substrate, and the resolution at which spatial predictors were extracted likely did not capture substrate variation at this fine scale. Additionally, limited observations of this assemblage were available.

Vertical connectivity between shallow and deeper reefs has been an important focus of recent studies, and is essential to assess the potential refugia and reseeding function of MCEs (Holstein et al., 2016). With statistically distinct assemblages,

this study provides evidence of limited vertical connectivity between the surveyed deeper reefs. However, the nMDS plots and habitat suitability maps revealed that the mesophotic assemblages (30 m, 60 m and 120 m) had some overlap and were distinct from rariphotic systems. These overlaps are driven to some extent by depth-generalist species found across multiple depths (Table 4.2). The limited structural connectivity between MCEs and rariphotic reefs reflects results from other regions that MCEs are biologically unique systems (Stefanoudis et al., 2019). Further research incorporating high-taxonomic resolution data along the depth gradient is necessary for reliable inferences on actual connectivity.

4.4.2 Geomorphology as a proxy for WIO deeper reef occurrence

Geomorphology is a key driver of hard bottom habitat and coral reef systems across all depths (Goreau & Goreau, 1973; Yesson et al., 2012). Studies focusing on the geomorphological patterns driving deeper reef occurrence have primarily been conducted in other geographies than the WIO, and primarily focus on MCEs rather than rariphotic ecosystems. As findings on drivers of rariphotic systems were less reliable, this study equally focuses on MCEs. Research in US waters containing the US Caribbean, Hawaii and the Gulf of Mexico demonstrated that geomorphological structures resulting from past sea-level change around islands drive mesophotic reef colonization (Locker et al., 2010). Seascape structures including carbonate mounds (Silva & MacDonald, 2017), paleo-shorelines, escarpments and terraces (Locker et al., 2010) and shelf edges (Smith et al., 2016) are of demonstrated importance for MCE habitat. Effects of relic topographic structures have also been demonstrated on the Great Barrier Reef (GBR) and Pacific, where MCE assemblages have been linked to the presence of submerged reefs (Bridge et al., 2011b, 2012) and submerged banks (Linklater et al., 2016) and the Red Sea, where submarine terraces support biodiverse MCEs (Weinstein et al., 2020). Likewise, a first study in the WIO indicates steep slopes and submarine walls may function as a priority habitat for MCEs (Osuka et al., 2021).

Our findings confirm that in the WIO geomorphology exerts control on the occurrence and distribution of mesophotic reef assemblages. High MCE occurrence probabilities were linked to relief features at all sites that provide topographically complex habitat and hard substrates for colonization at suitable depths. This indicates that topographic structures formed through historical sea-level patterns function as a proxy of suitable topographic MCE habitat. Importantly, paleo-shorelines at 120 m depth, likely formed during the Last Glacial Maximum about 20,000 years ago, at the investigated locations were associated with high probability occurrences of assemblage 3. Submarine terraces along the insular shelf of St Joseph and Aldabra were also associated with high occurrence probabilities of assemblages 2 and 3, reflecting a second MCE proxy feature previously reported in the literature (Sherman et al., 2010; Weinstein et al., 2020). MCE assemblages occurring on shelves (30 m-60 m) at all sites were linked to raised relief features (4.8, Appendix C.6). For example, the insular shelf at Aldabra contained elevated ridges extending along the slope, which provided hard substrate associated with higher probability occurrences of MCE habitat. The consistency between sites indicates that identified assemblage-environment relationships might hold for other coralline atolls in the region.

4.4.3 Methodological considerations

Due to the challenges associated with extensive sampling in environments beyond SCUBA depth, the sampling scheme was spatially limited and, because of choices made in expedition sampling strategy, depth segregated. Future surveys could use a revised protocol to provide more information on species turnover and environmental conditions between used sampling depths, for example, through vertical transects along the depth gradient. Data collection practices influenced the quality of the predictor variables. Multibeam data was acquired on a small tender, which was sensitive to motion artefacts. These artefacts were less pronounced in 25 m- and 10 m-resolution data layers than in 2 m-resolution data layers, which, in addition to the importance of the wider terrain, may contribute to their larger variable importance. Further, optimising the survey strategy to collect good quality backscatter data would allow to obtain more reliable data on

substratum characteristics, which may be linked to benthic habitat (Trembanis et al., 2017). Apart from the terrain variables considered in this study, other environmental factors not captured or captured as proxies also influence habitable space. These include biological processes as competition, predation and herbivory (Kahng et al., 2010) and oceanographic parameters like water chemistry, upwelling, wave and current action. In the Indian Ocean, the monsoon regime has a strong influence on reef development and recruitment through these factors (Gischler et al., 2014). Future studies could benefit from incorporating biotic and oceanographic parameters in similar analyses.

The choice of model building and evaluation method is important as different algorithms fit different relationships and tolerance constraints between biological and environmental data. This study confirmed that random forests and boosted regression trees are suitable tools to quantify the effect of multiscale interacting environmental drivers on the occurrence and distribution of deeper reefs. However, although high model accuracy and consistent results were obtained, caution is required when these predictive maps are to be generalised for marine management applications as presented maps do not take the spatial distribution of model errors and uncertainty into account (Lecours, 2017). RF and BRT spatial predictions were consistent in extent but differed in intensity. Upon visual inspection, BRT models appeared less reliable than RF models. This may be linked to the boosting characteristic of BRTs, as the sensitivity and effect of data artefacts can be additive over many model iterations (Sexton & Laake, 2007). Results for assemblage 4 also show that, despite high traditional model performance metrics, spatial autocorrelation in model residuals and the low number of observations may have underestimated model errors and resulted in erroneous relationships, such as the unreliable relationship with backscatter data. Finally, this study highlighted the importance of considering scale-effects by showing that the spatial resolution at which a predictor is calculated influences model responses and variable importance.

4.4.4 Conservation implications

There are few specific conservation efforts targeting mesophotic and rariphotic reefs globally, yet these reefs are of value to conservation and meet the criteria to be

classified as Ecologically or Biologically Significant Marine Areas (EBSAs) under the Convention on Biological Diversity (CBD) (Soares et al., 2020). Several key knowledge gaps limit evidence-based conservation and management of deeper reefs, including information on assemblage composition, drivers of occurrence and distribution and vertical connectivity (Turner et al., 2019).

Our results contribute to filling some of those knowledge gaps for deeper reef seascapes in the WIO and have been presented to Seychellois stakeholders involved in marine management and conservation. Deeper reefs are of particular interest for marine managers in Seychelles for their possible role as refuges for fish species of socio-cultural and economic value such as groupers and snappers (Tyler et al., 2009). Key take-aways from these conversations are that further application of predictive mapping approaches offers potential to maximise the information obtained from seascape structure and geographically dispersed mesophotic observations and to produce spatial predictions of suitable habitat in the WIO. Further, these results provide baseline information on the geomorphological factors that shape mesophotic reef distribution in the WIO and confirm findings from other regions and anecdotal observations that complex geomorphological structures as paleo-shorelines and terraces may act as proxies for mesophotic assemblages. The consistency between the results obtained per site, despite changing geomorphologies, suggests robustness of results and is an indication that similar relationships may exist across other Seychelles' Outer Islands where detailed biological survey data may be unavailable. This is important for a large ocean nation like Seychelles where country size and funding availability limit extensive biological surveys to locate deeper reefs throughout the territory. Obtained findings provide a starting point for marine managers to investigate possible target locations for further studies, and to assess whether these structures also form priority habitat or refuge for vulnerable or commercially important fish species within Seychelles. Establishing the importance of deeper reef habitats for these species, or a species that they feed on, is a key step towards putting these habitats under consideration for a measure of protection.

Although obtaining quantitative data of these, often remote, systems remains a critical bottleneck in informing conservation and management, as the costs of robotic

tools as AUVs decrease and interest in MCEs grows, data on these systems will become increasingly available (Armstrong et al., 2019; Osuka et al., 2021). Combined with predictive mapping approaches, these form valuable tools to provide important baseline information assessing the character and potential distribution of unexplored MCEs.

4.5 Conclusion

Combining terrain metrics derived from bathymetry, underwater video surveys of benthic deeper reef assemblages and machine learning techniques, this study demonstrated that continuous terrain structure can act as a reliable predictor for the occurrence and distribution of mesophotic benthic habitat. Depth, distance to shore, topographic complexity, slope and curvature, linked to geomorphological features, were the main predictors, but their relevance differed between assemblages.

Author Contributions

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Author contributions are as follows: DS - conceptualization, data curation (MBES), methodology, formal analysis, writing – original draft, writing-review & editing. PS and NF: data curation (field data acquisition, benthic ID), writing-review & editing. LW: supervision, methodology (expedition survey design), writing-review & editing. SP, VH: supervision, writing-review & editing.

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5 Fine-scale seascape heterogeneity shapes mesophotic fish assemblages

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 m, 60 m 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 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 substrate 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 will that are both ecologically meaningful to fish and operationally relevant to conservation strategies.

5.1 Introduction

Mesophotic coral ecosystems (MCEs), typically found in tropical and subtropical regions at water depths between 30 m and 150 m (Hinderstein et al., 2010), form important fish habitat (Blyth-Skyrme et al., 2013; Lindfield et al., 2016; Rocha et al., 2018). MCE associated fish consist of a shallow mesophotic community, that can sometimes include fish species also found on shallow reefs, and a specialist lower mesophotic community (Baker et al., 2016; Blyth-Skyrme et al., 2013; Rocha et al., 2018). They may be sites for large transient fish spawning aggregations, which create hotspots of productivity and trophic cascades through the ecosystem (Pickard et al., 2016). With increasing fishing pressure, scientific attention has also shifted to their potential role as refuges for endangered or fishery-targeted species (Kahng et al., 2017; Lindfield et al., 2016). Despite their importance, 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). Fish are mobile and respond to environmental heterogeneity at multiple spatial scales corresponding to their movements and habitat use, and knowledge of these patterns might therefore provide ecologically important insights (Borland et al., 2021). Yet, multiscale benthic habitat heterogeneity is rarely quantified across deeper seascapes as MCEs, with little known about its ecological significance to MCE fish assemblages (Swanborn 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; Sherman et al., 2019) recognised as key drivers of MCE fish distribution.

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 (Swanborn et al., 2022; Wedding et al., 2011). To date, no studies have combined these categories of spatial pattern metrics to quantify the effects of seascape composition, configuration and terrain structure on MCE fish assemblages. Yet, benthic composition, particularly live coral cover, and abiotic components such as hard substrate, have been reported to influence fish distributions in MCEs (Asher et al., 2017a; Jones et al., 2020; Kane & Tissot, 2017; Quimpo et al., 2019; Stefanoudis et al., 2019). The effect of the spatial arrangement of substrate types (such as aggregation/clumping, distance to each other) has not been investigated as a driver of fish assemblages, although the geographic context of habitat types has been reported to influence MCE fish assemblage structure (MacDonald et al., 2016; Pearson & Stevens, 2015). In addition to two-dimensional patch-based patterns, habitat complexity provided by geomorphological characteristics (Asher et al., 2017b; Bryan et al., 2013; Weijerman et al., 2019) and benthic communities (Gress et al., 2018) appear to play an important role in structuring and supporting MCE fish communities but approaches to measure MCE habitat complexity remain predominantly qualitative or categorical (e.g. Asher et al. (2017b); Pearson & Stevens (2015). 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 ($<$ 30m depth) and deep-sea ($>$ 200 m depth) coral reef fish (González-Rivero et al., 2017; Price et al., 2019).

Although knowledge and interest in the biodiversity and conservation of MCEs is increasing globally (Holstein et al., 2019; Soares et al., 2020), MCEs in the WIO remain particularly understudied (Pyle & Copus, 2019). Studies focused in the region have provided important insights in fish-habitat associations on shallow-water reefs (Osuka et al., 2018; Samoilys et al., 2019), but it is unclear how fish on deeper reefs relate to benthic environmental heterogeneity. This study aims to quantify and assess the combined effect of broader scale drivers (depth, geographic location) and fine-scale (cm-m) habitat heterogeneity on MCE fish assemblages by focusing on MCEs from geographically separated coral atolls in Seychelles, Western Indian Ocean (WIO). Using a combination of video-based fish transect surveys and high-resolution underwater photogrammetric reconstructions of benthic seascape structure from which habitat composition, configuration and terrain structure were quantified, this study investigated: 1) groupings of WIO 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. Following shallow reef findings (Wedding et al., 2019), a combination of metrics measuring habitat composition, configuration and terrain complexity is expected to be most appropriate to explain hierarchical structuring of MCE fish assemblages.

5.2 Methods

Seven research sites around six coral atolls of the Outer Islands of Seychelles were surveyed in March-April 2019 (Fig. 5.1) during the First Descent: Seychelles expedition (Woodall & Rivers, 2019). Aldabra, Astove, Alphonse and Desroches were located off the Amirantes Bank, although the later was located close (16km) 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 m, 60 m and 120 m depth contours. Each survey was 250 m long and run 1-2 m above the seabed at a speed of approximately 0.2 knots where possible. The position of the submersible was recorded using a Kongsberg HiPAP 501 USBL system.

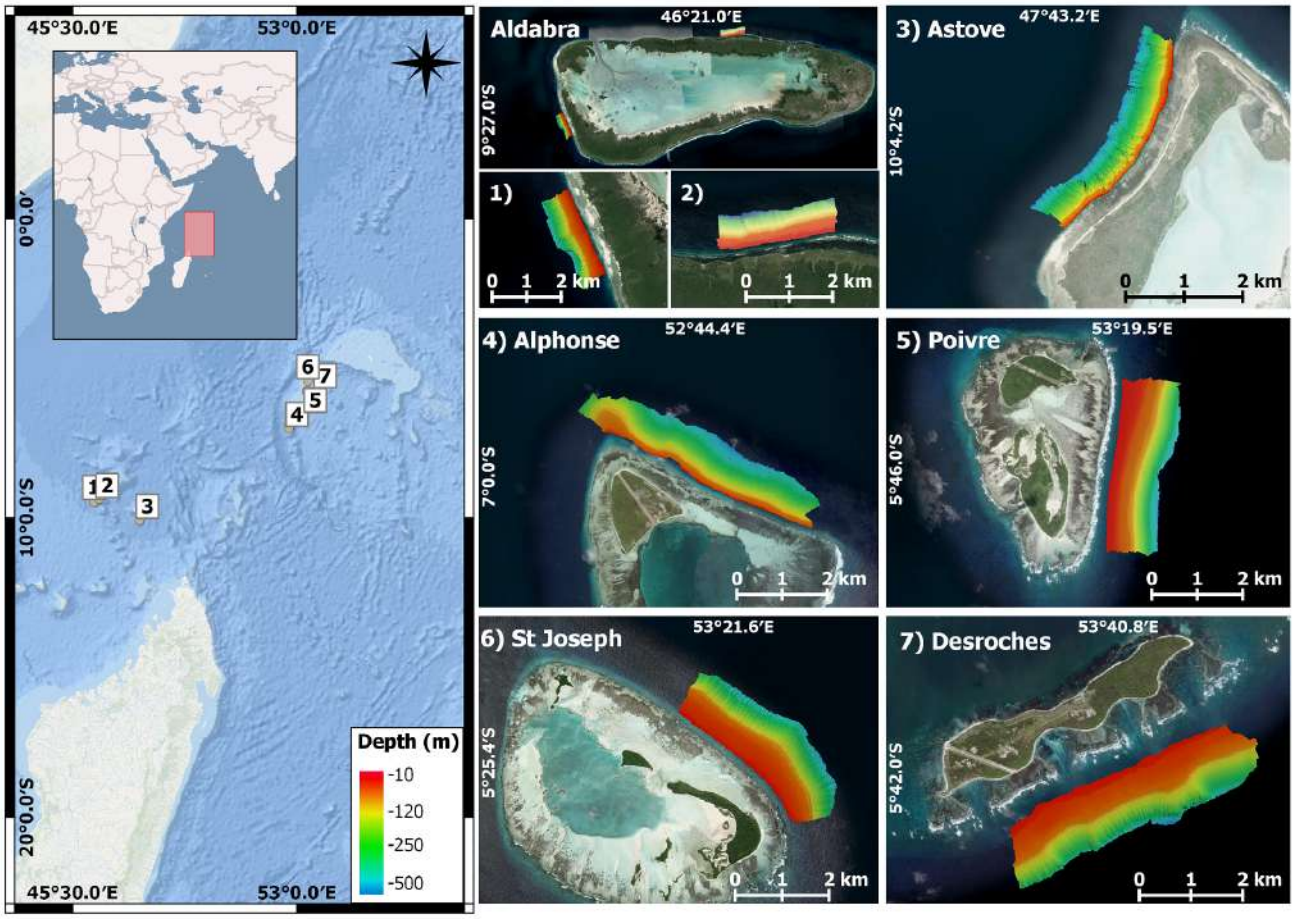


Figure 5.1: Map of locations surveyed during First Descent: Seychelles expedition in 2019

5.2.1 Remotely sensed data

Fifty-metre transects for photogrammetric reconstructions (Fig. 5.2) were extracted from the video survey's 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 WIO fish surveys (Osuka et al., 2018; Samoilys et al., 2019). Photo frames were extracted from downward-facing video every 2 seconds using FreeVideotoJPG converter (DVDVideoSoft, 2018), linked to transect USBL position using time stamps, 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 Table D.1.1 in Appendix D). When transects were reconstructed using data from the same 250 m video survey, they were spaced at

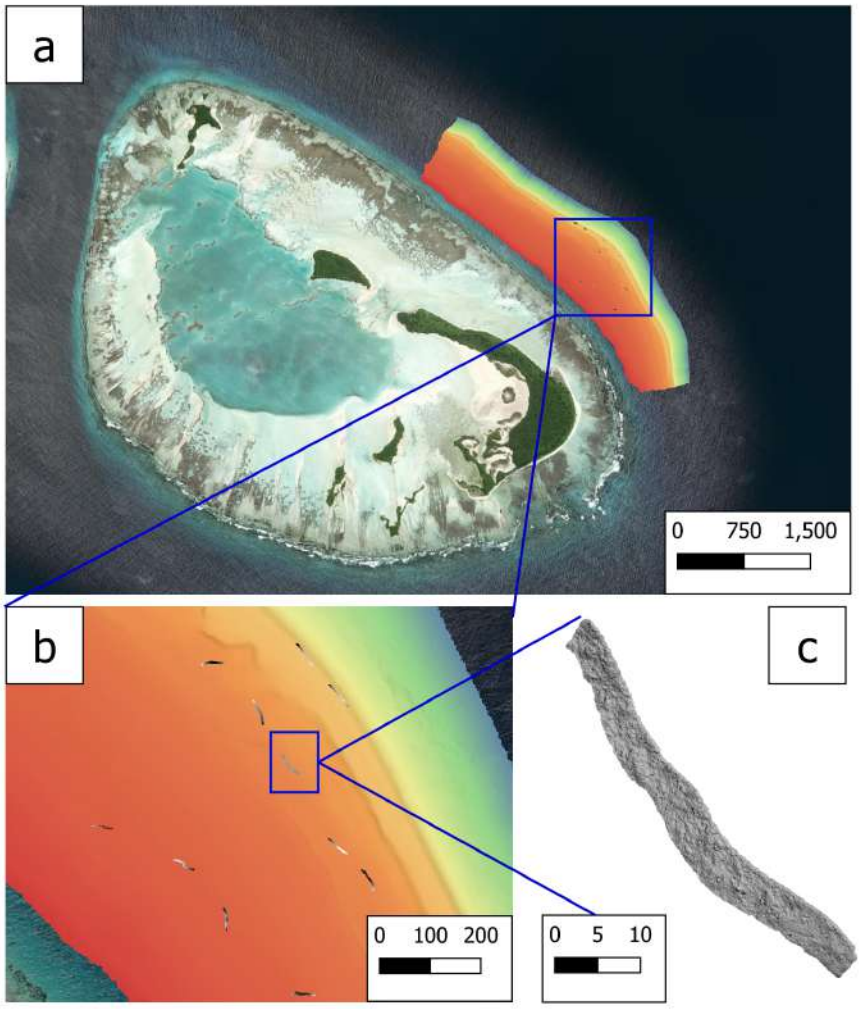


Figure 5.2: Example of photogrammetry transect reconstructions conducted at St Joseph. (a) shows an overview picture of the site, (b) shows transect locations at the three different depths (30 m, 60 m and 120 m) plotted on the bathymetry, and (c) represents a close up of a transect. Scale is in meters.

least 25 m apart to maintain separate sampling units (Fig. 5.2b). SfM reconstructions were cropped to a maximum width of 5 m before constructing DBMs and orthomosaics 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

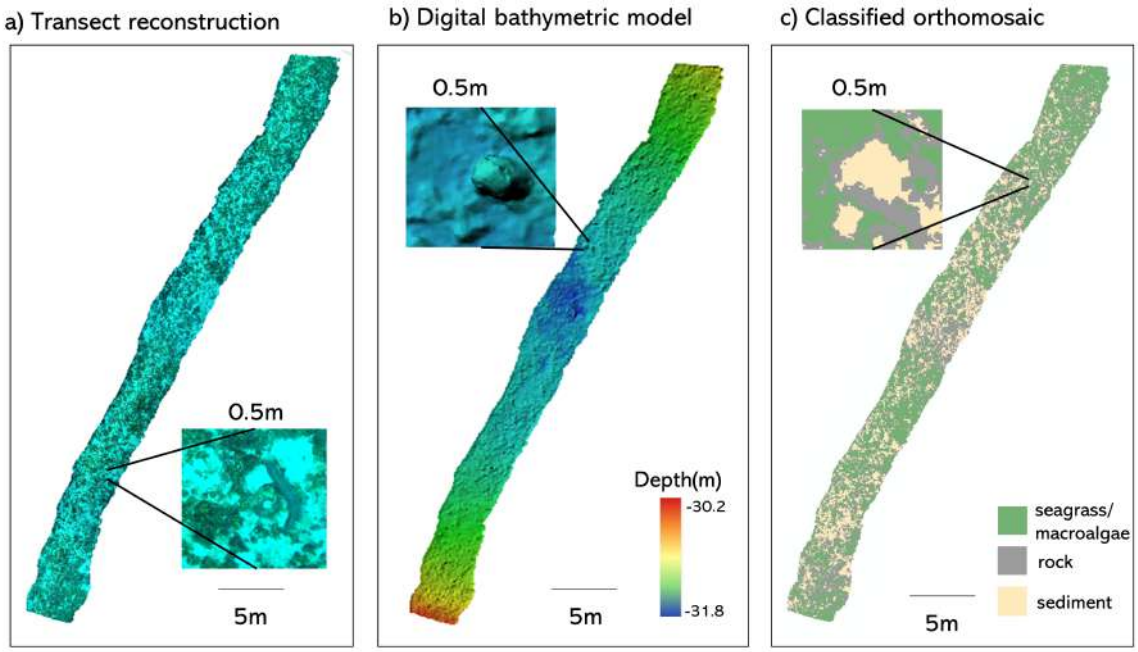


Figure 5.3: Outputs of environmental data extraction. SfM photogrammetry produced a reconstruction of a transect (a; Poivre, 30 m), from which a 3D reconstruction (b) and an orthomosaic were exported. The orthomosaics was classified into major substrate types present (c)

horizontal plane, after which the orthomosaics and DBMs (Fig. 5.2b, c) were exported at multiple resolutions, representing de-trended benthic features of multiple sizes (1 cm, 5 cm, 10 cm, 15 cm and 20 cm), to evaluate any scale-dependent responses of fish assemblage composition to seascape structure (Weijerman et al., 2019).

Terrain structure

Terrain derivatives measuring orientation, curvature and topographic complexity were extracted from these multi-resolution DBMs with a focal window size of 3x3 pixels (Fig. 5.3b), using the R raster (Hijmans, 2017) and SpatialEco (Evans, 2017) packages (Table 5.1), and calculated using the mean value per transect. As the lack of attitude data prohibited the calculation of absolute slope values from the DBMs, but slope is an important variable for mesophotic fish assemblages (Osuka et al., 2021), mean slope value for each transect was instead calculated from bathymetric data collected by multibeam echosounder and gridded at 2 m x 2 m (Fig. 5.1, details about multibeam bathymetry data were presented in Chapter 4), also used to measure distance to

shore in QGIS 3.12.

Patch metrics: composition and configuration

Orthomosaics were imported into ArcMap 10.6 for maximum likelihood classification using the image classification toolbar of the Spatial Analyst toolbox. 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 (poorly lit) transects were excluded as this compromised the ability of the tool to identify substrate classes accurately. Multiscale classified files (Fig. 5.3c) resulting from the maximum likelyhood classification were imported into FragStats version 4.2.1 (McGarigal et al., 2012) to quantify seascape composition and configuration over the entire transect (as opposed to individual patches or classes) (Table 5.1).

Table 5.1: Predictor variables created from photogrammetric reconstructions. The right column shows variables retained for analysis

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

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

5.2.2 Fish assemblage data

Fish occurrence and total length were continuously recorded using EventMeasure (SeaGIS) software (Seager, 2014) from forward-facing survey video (Stefanoudis et al., in review). Fish were identified to the lowest taxonomic level possible, the majority of which were species-level, and subdivided into trophic groups (Table 5.2) as a proxy for their functional role (Osuka et al., 2018; Samoilys et al., 2019). Biomass was calculated using published length-weight relationships on FishBase (Froese & Pauly, 2020).

Fish observations at the locations of photogrammetric transect reconstructions were extracted from the overall video survey using time stamps. To enable subsequent statistical analysis, transects were excluded from the analysis when only unidentified fish were present, or when fewer than three fish were observed. The remaining assemblage and biomass datasets contained observations on 6538 individuals of 76 fish species. 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) and dominant trophic ecological processes following previous studies in the region (Osuka et al., 2018; Samoilys et al., 2019). The third contained transect-level descriptive data (total abundance, Shannon diversity, trophic group richness, biomass, and assemblage

Table 5.2: Trophic groups, descriptions and characteristic Western Indian Ocean species

Trophic group	Assumed trophic role	Selected WIO taxa observed
Planktivores	Reef associated fish feeding on planktonic food in water column	Acanthuridae (*A. thompsoni*, large *Naso* sp.) Balistidae (*Melichthys spp., Odonus niger*) Caesionidae Serranidae (*Pseudanthias sp.*)
Piscivores	Top level predators, exert control on fish of lower trophic levels, often species of interest to fisheries	Carangidae Lutjanidae Serranidae
Herbivores	Feed on benthic primary producers thereby controlling coral-algae system. Can be further subdivided according to feeding method (excavator, scraper, browser, grazer, grazer-detritivore)	Acanthuridae (*Acanthurus* sp., apart from *A. thompsoni*, small *Naso* sp) Pomacanthidae (*Centropyge* sp.) Scaridae (*Scarus* sp., *Clorurus* sp.)
Invertivores	Feed on small invertebrates	Balistidae (*Sufflamen sp.* Chaedontidae (except corallivore species) Labridae (*Bodianus* sp., *Halichoeres* sp., *Labroides* sp.) Pomacanthidae (*Pomacanthus* sp.)
Omnivores	Highly diverse diets, generalist species, often species of interest to fisheries	Haemulidae Lethrinidae Lutjanidae (all apart from *Aprion virescens and Lutjanus bohar*
Carnivores	Consumers of both fish and invertebrates	Priacanthidae Scorpaenidae Serranidae (*Liopropoma* sp.)
Corallivores	Feed on coral polyps	Chaedontidae (*Chaetodon trifasciatus, C. ornatissimus, C. zanzibarensis*)
Detritivores	Feed on detritus in algal turf and sediment to extract nutrients	Acanthuridae (*Ctenochatus* sp.)

size structure (binned fish length observations, 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-50 cm, > 50 cm)). Unidentified fish were included in abundance counts but excluded from trophic group richness, Shannon diversity, and biomass counts.

5.2.3 Data analysis

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

Exploring fish assemblage groupings

Ward's clustering analysis based on Bray Curtis distance on fourth-root transformed transect abundance and 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). 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 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 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. Site scores of the separation of samples along the dbRDA axes indicated the influence of habitat characteristics on assemblage abundance and biomass differences. Associations between sites and environmental variables were visualised using biplots, where the length and direction of vectors indicate the strength and direction of 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'). RFs were chosen for their ability to fit complex responses from a large number of predictor variables, coping with interacting predictor variables and filtering out irrelevant predictors (Elith et al., 2008). 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 constructed using three repeats of 5-fold cross-validation to reduce overfitting. During the training process, the optimum number of trees and variables used for splitting at each node was optimised using the lowest value for the RMSE (root of the mean square error – the standard deviation of unexplained variance). Ten resamples of the final model were created for performance assessment using the mean and standard errors of R-squared 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 five most influential predictors.

5.3 Results

5.3.1 Assemblage groupings

The clustering analysis on transect fish abundance and biomass data revealed four distinct depth- and site driven groupings (Fig. 5.4). 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. 5.4a) split into two depth-driven groups: the 120 m transects and a combination of the 30 m 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 clusters were delineated, representing the 30 m 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 m 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 (Fig. 5.4b).

Subsequent assemblage characteristics comparisons provided further insight into the compositional differences between identified clusters (Fig. 5.5). Fish biomass per transect, but not abundance, was significantly ($p < 0.05$) higher in the 30-60 m clusters than deeper 120 m clusters at the same location. Moreover, both abundance and biomass were significantly ($p < 0.05$) higher in UM_OFF than UM_AM, but only biomass was higher in LM_OFF compared to LM_AM. In terms of trophic composition (Fig. 5.5a, 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 was used (Fig. 5.5c, 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 shallowest clusters (Fig. 5.5e, f).

Indicator species analysis revealed that 36 of the 76 species sampled were significantly associated with one of the determined clusters (Table D.2.1 in Appendix D). 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

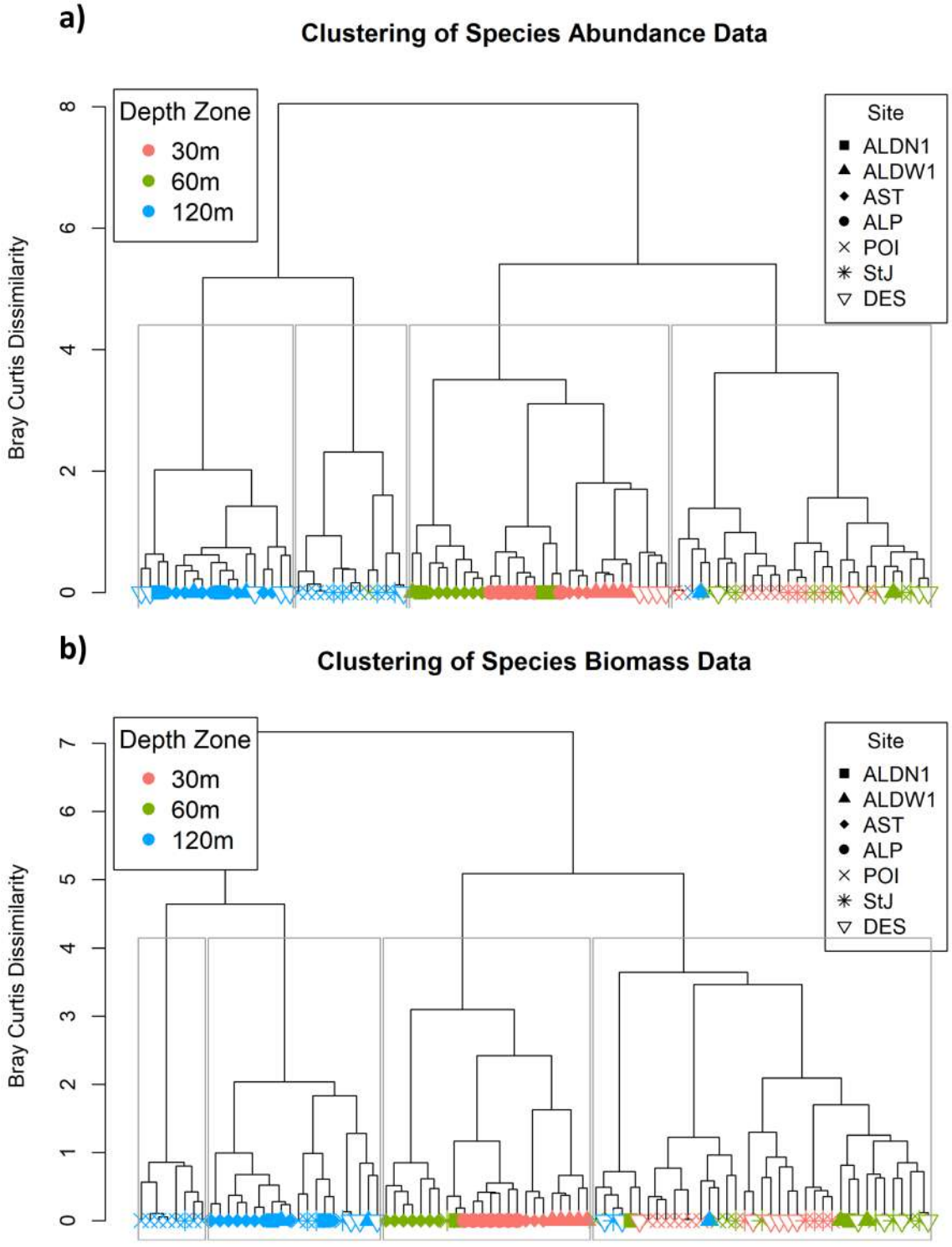


Figure 5.4: Clustering of fish abundance (a) and biomass (b) per transect where grey boxes delineate different clusters. Colours represent depth classes of observations. Symbols represent site, with closed symbols representing off-bank islands (Aldabra, Astove and Alphonse) and open symbols representing sites on and next to the Amirantes bank (Poivre, St Joseph and Desroches)

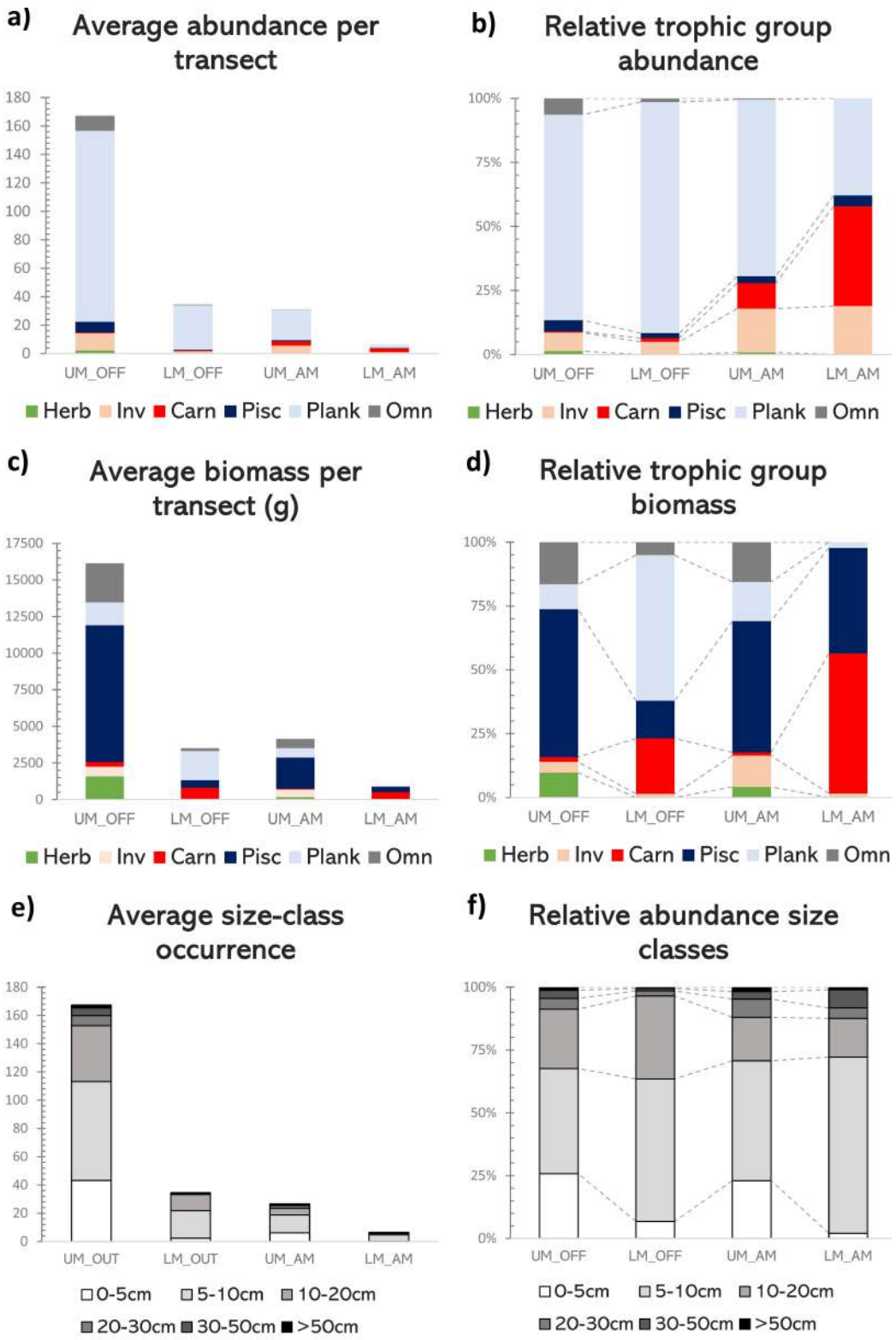


Figure 5.5: Composition of trophic groups per cluster, where UM_OFF and LM_OFF represent the 30-60 m observations and 120 m observations of off-bank islands and UM_AM and LM_AM represent the 30-60 m observations and 120 m observations of the Amirantes group. Upper panels show average group abundance 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).

carnivorous fish species (e.g. *Pseudanthias* spp., *Scorpaenodes* spp.), with a higher number of planktivorous species associated with LM_OFF.

5.3.2 Drivers of assemblage groupings

In addition to broad-scale environmental drivers (depth and site) also identified before (Fig. 5.4), fine-scale spatial terrain metrics describing habitat composition (substrate type), configuration (proximity index, contagion) and terrain structure (slope, VRM) were also statistically significant in explaining variation in assemblage abundance and biomass. Adjusted R-squared values showed 46.9% and 39.7% of the variation in abundance-based and biomass-based fish datasets, 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-based), with the additional inclusion of contagion, rubble and scleractinian coral cover in the abundance model (Table 5.3a), and distance to shore in the biomass model (Table 5.3b). Permutational tests (n=999) showed the significance of included variables . 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. 5.6a) and biomass data (Fig. 5.6b). The first 6 axes were statistically significant and further considered (Table D.3.1 in Appendix D). Environmental scores indicated which environmental variables each significant dbRDA axis represented (Table D.3.2 in Appendix D; Fig. 5.6). The first axis contained depth and slope, representing the shallow to deep gradient and transition from gently to steeper sloping environments. The second axis, 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. The third dbRDA axis represents a gradient from sparse distributions of small patches to clusters of large patches (proximity index), structural complexity (VRM) and sediment.

Table 5.3: Variables included in abundance (a) and biomass (b) dbRDA. Stars indicate a significant contribution of the variable

a) ANOVA Abundance dbRDA	**df**	**Sum of Squares**	**% total variance**	**P value**
Site*	6	8.987	24.13	<0.001
Depth*	1	5.295	14.22	<0.001
Vector Ruggedness Measure*	1	1.5324	4.11	<0.001
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) ANOVA Biomass dbRDA	**df**	**Sum of Squares**	**% total variance**	**P value**
Site*	6	8.675	23.81	<0.001
Depth*	1	4.3784	12.02	<0.001
Vector Ruggedness Measure*	1	1.5089	4.14	<0.001
Macroalgae / seagrass *	1	11.1707	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
Distance to Shore*	1	0.4893	1.34	0.012
Residual	77	19.8226	54.40%	

The fourth dbRDA axis represented percentage cover of macroalgae and/or seagrass, the fifth contagion (abundance) and the sixth further site-dependent variation.

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. The biomass ordination plot (Fig. 5.6b) showed a larger spread, indicating more pronounced differences between transect biomass data than abundance data. Ordination ellipses around observations in each assemblage allowed for a further description of assemblage-specific environmental conditions. UM_OFF was found on sloping and complex terrain characterised by

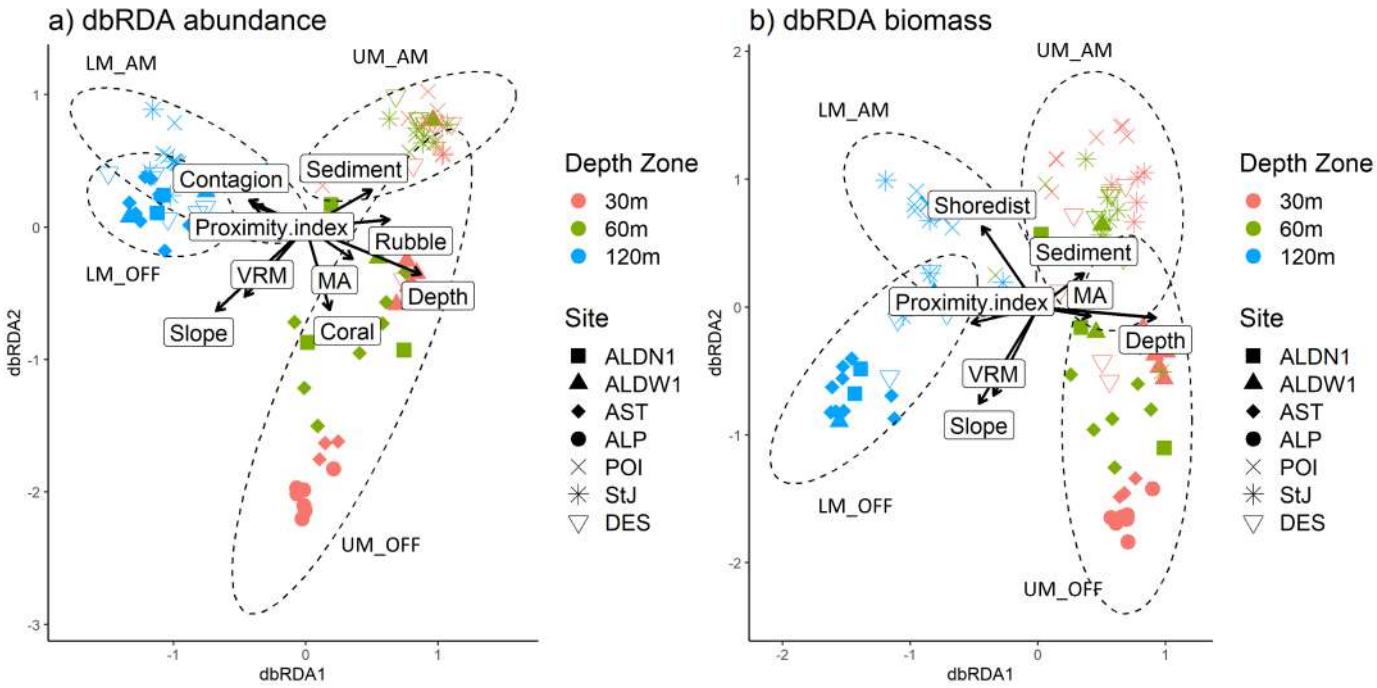


Figure 5.6: Ordination biplot of species abundance (a) and biomass (b) per transect as a function of dbRDA1 (17.72% variance abundance and 14.37% biomass) and dbRDA2 (10.94% variance abundance and 9.68% biomass). Point colours show the depth zones of transects, whilst point shapes show the site at which each transect was conducted. Continuous environmental variables included in model have been super-imposed as vectors displaying the strength (represented by vector length) and direction of their effect, with depth included as a negative variable. Site was included as a categorical variable. Ordination ellipses indicate identified assemblage clusters.

macroalgae/seagrass and live coral. LM_OFF was found on terrain of similar structure, but on a more homogeneous substrate environment composed mainly of bedrock (associated with depth, Table 5.2). 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 substrate types (coral, macroalgae/seagrass, sediment and rubble) was larger for abundance than for biomass (only sediment and macroalgae/seagrass).

5.3.3 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 somewhat variable proportion of variance (mean 0.62, sd 0.07) (Fig. 5.7). MAE values (Fig. 5.7B-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 comparable to similar investigations using machine learning techniques in shallow reefs (Costa et al., 2014; Pittman et al., 2009). Obtained values were considered adequate as variations in fish assemblages are also driven by characteristics in the overlying water column, which could not be quantified in this study.

Variable importance

Variable importance plots (Fig. 5.8) revealed that final models were composed of combinations of predictor variables, with no clear patterns across assemblage characteristics. Partial dependence plots (Appendix D.4) showed the effects of the five most important variables on assemblage characteristics. Within UM_OFF (Fig. 5.8a, Fig. D.4.1), more aggregated and connected habitat types (contagion, proximity index) were strongly associated with abundance, biomass and diversity, whilst a higher proportion of sediment was positively associated with diversity and functional richness. In LM_OFF (Fig. 5.8b, Fig. D.4.2), structurally complex (VRM) and fragmented habitats (division) with an increased proportion of sediment drove fish abundance, diversity and functional richness and more aggregated habitats (contagion) were important in maintaining fish biomass. In UM_AM (Fig. 5.8c, Fig. D.4.3), structurally complex habitats drove functional richness, whereas habitats with higher proportion of live coral increased fish abundance. In LM_AM (Fig. 5.8d, Fig. D.4.4), structurally complex (VRM) and curved terrain (TPI) drove diversity, functional richness and abundance. Biomass and functional richness were strongly dependent on depth.

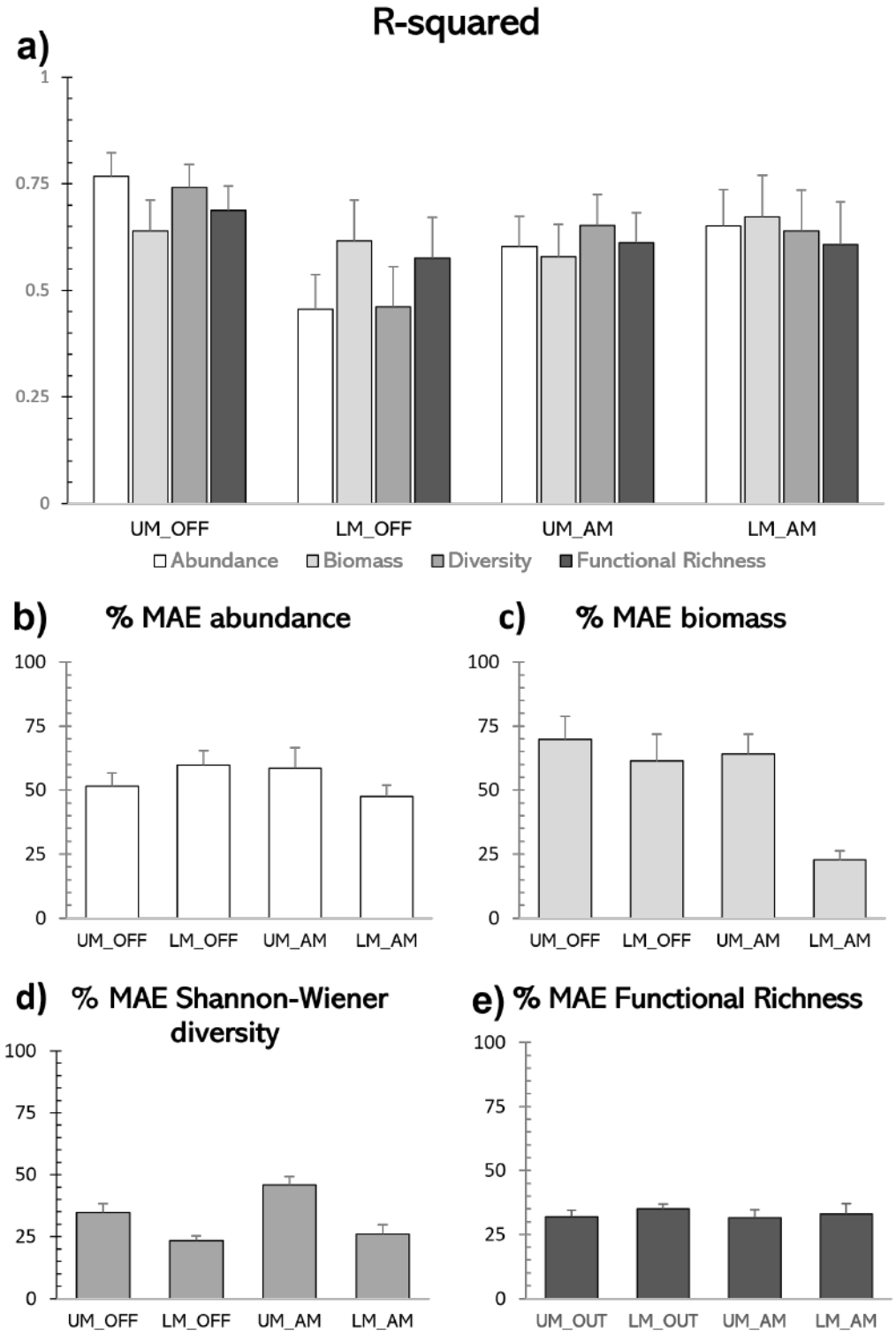


Figure 5.7: Performance of Random Forests (±SE) for species abundance, biomass, Shannon diversity and trophic group richness in the four clusters measured using R-squared (a) and standardised MAE (b-e). UM represents clusters composed of 30 m and 60 m transects, LM represents clusters composed of predominantly 120 m transects and OFF and AM refer to offshore islands and Amirantes group observations respectively.

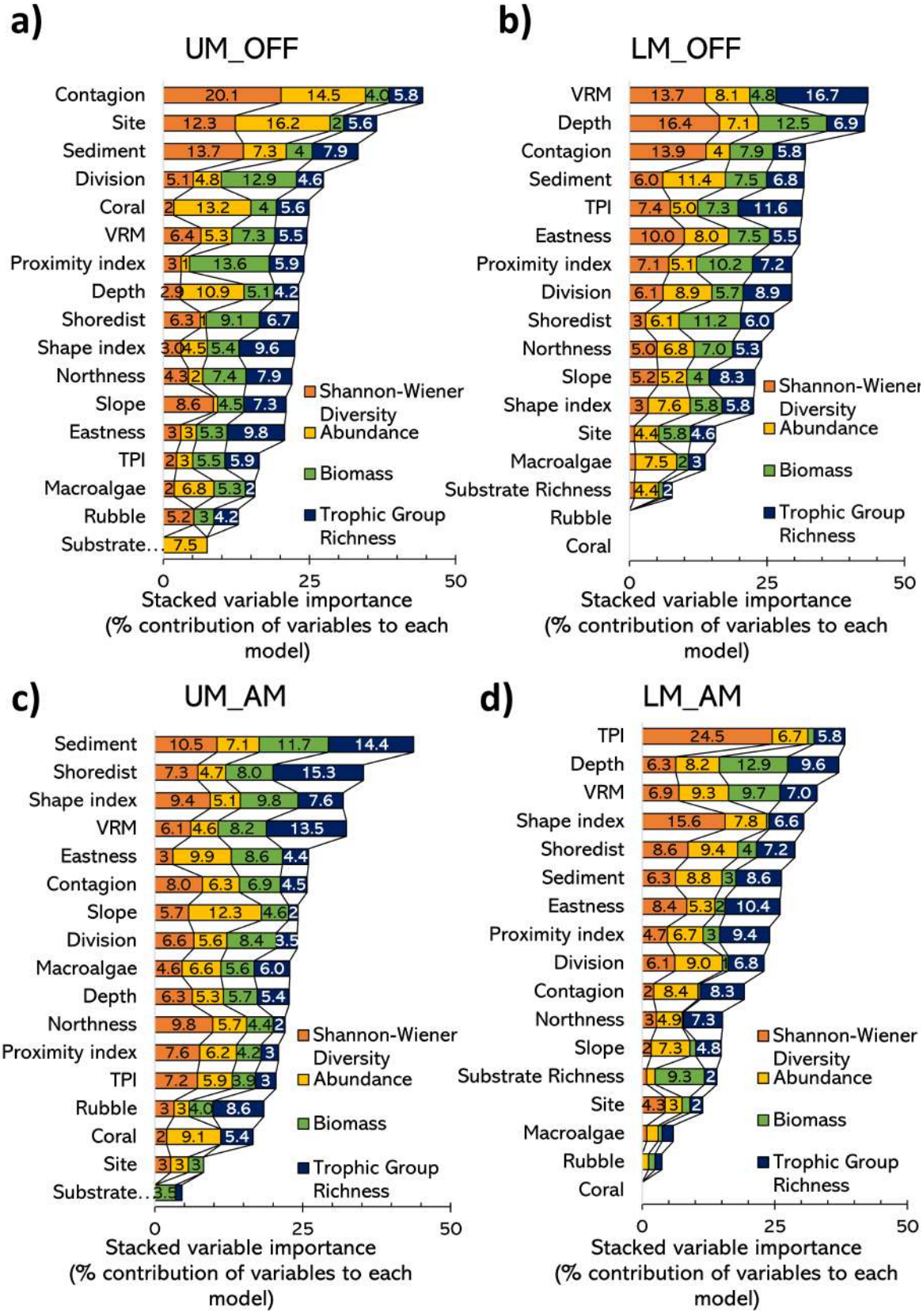


Figure 5.8: Variable contributions to model assemblage characteristics for UM_OFF (a), LM_OFF (b), UM_AM (c) and LM_AM (d). Variable contributions were standardised to a percentage of the overall assemblage descriptor model and stacked to evaluate variable importance across models

5.4 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 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 across mesophotic depths (30 m, 60 m, 120 m). The findings highlight a need to develop research and monitoring programmes explicitly incorporating environmental data across spatial scales to improve insights in the ecological effect of mesophotic habitat heterogeneity.

5.4.1 Mesophotic fish-habitat associations

Broad-scale assemblage groupings

Assemblages were separated along gradients of depth, site and geomorphology. Depth is a well-established driver of MCE fish assemblage and trophic structuring and 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 m-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 m and 120 m and therefore the transition of fish assemblages may also be gradual. Observed shifts in the relative abundance and biomass of trophic groups across the depth gradient match those previously discussed in literature in other regions. Schooling planktivores form a large proportion of MCE fish abundance and biomass in the 30-60 m zone in multiple geographies (Kahng et al., 2010), which may in turn drive the presence of piscivores and omnivores that feed on these planktivorous species (Stewart & Jones, 2001). The well-known decline of herbivores along the depth gradient matches decreases in

reef-building scleractinians (Stefanoudis et al., 2019)and macroalgal coverage (Andradi-Brown et al., 2016) and links to a trophic shift to carnivory at lower mesophotic depths (Kahng et al., 2014). Fishing pressure typically decreased activity at mesophotic depths (Lindfield et al., 2016), which may contribute to the increased numbers of larger-bodied individuals in 30 m and 60 m clusters.

Species assemblages vary across geographic locations because of regional differences in environmental conditions, connectivity and historical use patterns (e.g. fishing) (Samoilys et al., 2019). Regional differences in WIO 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. 5.1), 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). Additionally, Aldabra has been afforded long term marine protection which may contribute to these differences, but 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). 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 and is consistent with the lower abundance and biomass of reef-dependent fish.

Local assemblage structuring

Fine-scale variations in terrain structure, composition and configuration had variable effects on identified assemblages.

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 was important in explaining inter-assemblage variations. Distinct substrates were associated with 30-60 m (sediment, coral, rubble, macroalgae) and 120 m (bedrock, 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. As fishes use multiple environments, patch-mixtures including sediment can positively influence fish assemblages (Sievers et al., 2020).

Configuration metrics measured the spatial arrangements of patch types, and results suggest that assemblage responses to the spatial characteristics of the seascape

differed between mesophotic assemblages at 30-60 m and 120 m depth. 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 at transect-scale, 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, 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 substrate patches tend to be more extended and well-connected.

5.4.2 Methodological considerations

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. The effect of the overlying water column is likely to be pronounced in the surveyed MCEs, as the majority was located on steep slopes. Here, currents influenced HOV navigation, and effects were visible in video imagery with frequent deviations in heading. 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 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. Although home ranges of smaller fish might be within the spatial scale covered in this study, larger-bodied fish will have home ranges that exceed the 50 m x 5 m areas covered here, which might compromise

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 in the effects of context and potential connectivity between habitats. For example, this could be realised using measures of terrain structure, habitat composition, and configuration derived from broader scale habitat maps of the area (Proudfoot et al., 2020).

The specifics of the sampling regime may also contribute to unexplained variation. It was not possible to measure all habitat conditions per site because of the limitations associated with extensive sampling in deeper environments . Additionally, there are biases associated with all fish sampling methods, including video transects conducted with underwater vehicles. Specifically, conducting video transects using an HOV may result in avoidance or fleeing behaviour of fish (Stoner et al., 2008), and underwater vehicles could be less successful at recording fish species on steep slopes and hiding within crevices (Osuka et al., 2021), compromising the ability to record all individuals originally present at a location.

5.4.3 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). To realise such efforts, technological advances in monitoring options and an improved understanding of the multiscale environmental drivers of MCE habitat and their effects on associated fish assemblages are necessary. This study contributes to closing these knowledge gaps in different ways and all findings on habitat associations of MCE fish at different depth zones uncovered in this study were shared with stakeholders from the region.

First, this study confirmed that SfM photogrammetry approaches, extensively applied to measure habitat complexity in SWRs, can be extended to MCEs. Although the logistical challenges of obtaining MCE video surveys through underwater vehicles or technical diving remain, this study showed SfM photogrammetry can be used effectively to map MCE habitat using data collected during MCE video surveys. Although no key

adaptations to survey protocol were required, changes in light conditions (e.g. shading), sedimentation and currents offsetting the underwater vehicle's heading may influence reconstruction success. SfM photogrammetry may also be a valuable approach to apply to data collected using low-logistics AUVs, which have recently been advocated as an important approach to collect data on MCEs for marine management and conservation data-poor regions as the WIO (Osuka et al., 2021). Secondly, this study shows that seascape metrics applied to the dual outputs of SfM photogrammetry, orthomosaics and DBMs, are suited to study different aspects of spatial habitat heterogeneity. Monitoring programmes could benefit from incorporating spatial pattern metrics to identify where and when they change and to and evaluate possible implications for associated species and habitats (Wedding et al., 2011). Thirdly, seascape metrics provided key insights into habitat associations of MCE fish at different depth zones and possible priority features. Areas of high MCE fish abundance and biomass included sites with steep slopes and high terrain complexity, with upper and middle mesophotic habitat characterised by coral cover and connected patch mixtures, and lower mesophotic habitats with fine-scale habitat heterogeneity in topography and substrate types. These areas could form important targets for future surveying and monitoring efforts, as well as for fisheries.

5.5 Conclusion

This study extended landscape ecology approaches developed on land and increasingly applied in shallow water environments to fine-scale remotely sensed data on deeper reefs. Obtained findings indicate for the first time 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 across mesophotic depths (30 m, 60 m, 120 m). Findings highlight a need to develop research and monitoring programmes explicitly incorporating environmental data across spatial scales to improve insights in the ecological effect of mesophotic habitat heterogeneity. Methodologically, this study demonstrated the powerful and resource-effective combination of SfM photogrammetry and seascape metrics, and suggests this combination has potential for MCE monitoring and conservation.

Author Contributions

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Author contributions are as follows: DS - conceptualization, data curation (SfM photogrammetry), methodology, formal analysis, writing – original draft, writing-review & editing. PS: data curation (field data acquisition, fish ID), writing-review & editing. LW: supervision, methodology (expedition survey design), writing-review & editing. SP, VH: supervision, writing-review & editing.

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6 Discussion and conclusion

6.1 Discussion

Understanding biodiversity-environment relationships in heterogeneous environments is a priority in fundamental ecological research and conservation management of all ecosystems. Due to the challenges of studying marine ecosystems > 30 m deep, substantial knowledge gaps exist in our understanding of deep seabed environmental heterogeneity and its ecological implications, complicating the development of effective management policies and actions for these environments (Wright et al., 2018). However, advances in data acquisition and modelling and new theoretical frameworks offer many opportunities for generating new ecological insights on the character and effects of seabed environmental heterogeneity which should better support decision makers.

This thesis aimed to contribute an improved fundamental and applied understanding of spatial heterogeneity in deep seabed environments. It proposed seascape ecology as a theoretical framework and methodology to study environments beyond 30 m depth and identified several focal areas to improve the potential of these methods to address ecological knowledge gaps in the deep sea (Chapter 1). These focal areas formed the objectives of this thesis and were explored in case studies from seamounts and deeper reefs in the Western Indian Ocean, varying in observational and analytical scale and biological data availability. First, a strategy to quantify and compare seamount spatial heterogeneity from geomorphological class maps using metrics of composition and configuration was explored (Chapter 2). Then, resulting maps were used to examine the associations between commercially important fish and the composition and configuration of their surrounding environments (Chapter 3). With respect to deeper reefs, the capability of multiscale measures of terrain structure to function as a predictor of deeper reef assemblages was tested (Chapter 4). Finally, composition, configuration and terrain structure were combined to investigate which components of environmental heterogeneity shape mesophotic reef fish assemblage composition (Chapter 5).

This final chapter discusses the scientific contributions of this thesis by synthesising key findings and considering how these novel insights address the overall aim and specific objectives (Fig. 6.1). Additionally, it suggests further research themes that would logically build upon the work presented here to enable an improved understanding of seabed spatial heterogeneity and its ecological relevance, including for management, using concepts from seascape ecology.

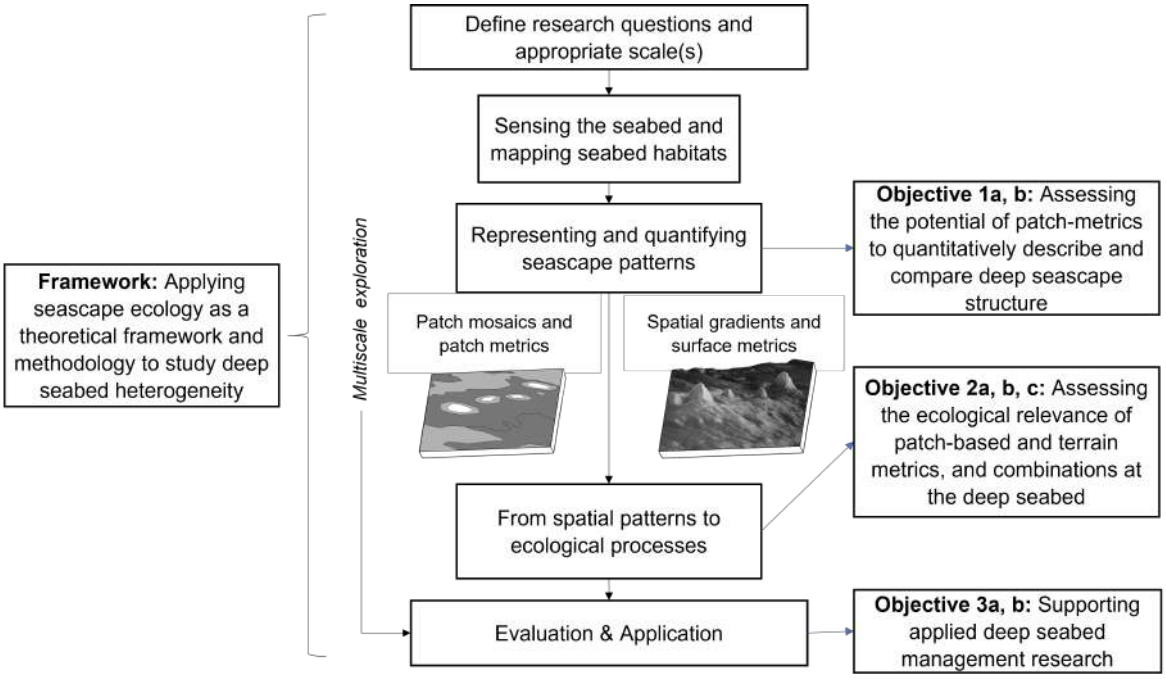


Figure 6.1: Recap of scientific objectives of this thesis and their links to the framework proposed in Ch1

6.2 Scientific contributions

6.2.1 Framework: Applying seascape ecology to study seabed heterogeneity

The first chapter provided a first comprehensive review of seascape ecology for seabed environments. It introduced seascape ecology, then proposed and explored a framework for its application in seabed environments > 30 m, and finally it highlighted future research areas to enable the wider application of seascape ecology in the deep sea. Drawing on examples, this foundational contribution (Appendix E.1) is intended

to function as a catalyst for new research and as a reference to help researchers explore seabed heterogeneity and its ecological relevance using seascape approaches. Overall, it provides a roadmap for future studies seeking to understand how seabed biodiversity may be affected by spatiotemporal variations in environmental factors such as geomorphology, substrate types and currents and the application of this information for marine spatial planning.

6.2.2 Theme 1: Quantifying seascape structure using spatial pattern metrics

Although implemented widely in shallow-water and terrestrial surveys, patchiness in seabed and habitat structure is not commonly quantified in seabed ecology studies using spatial pattern metrics.

Objective 1a: To assess the potential of patch-based metrics from categorical seabed habitat maps to quantitatively describe seascape structure

Case studies in this thesis demonstrated that patch-based metrics provide an effective tool to quantify the observable spatial patterns represented in habitat maps and can provide novel insights into the character of habitat heterogeneity.

At the SWIR seamounts, spatial pattern metrics allowed quantitative assessments of broad-scale (m-km) seamount seascape structure from geomorphological class maps. These were implemented for seascape sample units (10 km) and individual patch types (1-10 km), and in smaller focal areas around transects (500 m). Results demonstrated that spatial heterogeneity in geomorphology was strongly variable between seamounts. Like other environmental characteristics as depth, geographic location and oceanography (Clark et al., 2011), these variations are biologically relevant with consequences for the ecological processes that structure deep-water benthic habitats.

At the deeper reefs of Seychelles, patch-based metrics were applied to quantify relatively fine-scale (cm-m) seascape composition and configuration from orthomosaics produced using video data and SfM photogrammetry. Although SfM photogrammetry has been demonstrated as a successful technique to quantify fine-scale structural complexity on shallow (< 30 m) and deep water (> 200 m) reefs (Burns et al.,

2015; Robert et al., 2017), it has not been applied to study spatial heterogeneity in mesophotic reefs. This study was also the first to quantify both seascape composition and configuration from photogrammetry outputs. By producing visual maps of substrate types and benthic cover, this technique showed promise for quantifying biologically produced spatial heterogeneity, such as created by mesophotic and cold-water coral reefs, without the need for spatially predictive models (e.g. Goode et al. 2021).

By using different study systems, this thesis also demonstrated that patch-based metrics are applicable to multiple types of thematic seabed maps, greatly varying in the type of mapping technique used and their spatial extent and resolution. Applying patch metrics to quantify seascape composition and configuration represented in these thematic maps required no adaptation to mapping techniques or data collection protocol. In fact, data were collected on two different expeditions without an explicit spatial heterogeneity analysis in mind. This additional analytical step could also be directly applicable to categorical seascape maps produced using other techniques, such as terrain form maps using geomorphons (landscape elements, Jasiewicz & Stepinski (2013)), or bottom-up habitat maps. This can include incorporating other datasets representing environmental heterogeneity, such as oceanographic parameters (see also section 6.3.1.

Objective 1b: To assess the potential of patch-based metrics to compare seascape structure and associated communities between sites

Variations in benthic seascape composition and configuration likely have consequences for biodiversity and ecological processes at the seabed, but are rarely numerically compared (Swanborn et al., 2022). In addition to describing seascape structure, case studies demonstrated that patch metrics also provide a quantitative technique to compare seascapes.

At the SWIR seamounts, patch-based metrics were used to compare seamount seascapes in terms of the occurrence and distribution of individual patch types and overall seamount structure. The analysis provided a strategy to score seamount seascapes from low to high spatial environmental heterogeneity and showed that seamounts differed most notably in patch size, aggregation and interspersion. These results are consistent with a recent study on New Zealand seamounts (Goode et al.,

2021), which used spatial pattern metrics to quantify patch characteristics of mega-epibenthic communities, and found that similar metrics (number and size of patches, patch distances and patch connectedness) varied within and between seamounts. In MCEs, comparisons of transect spatial structure quantitatively showed that benthic composition and configuration differed between transects surveyed. Along depth gradients and geographic location, transects differed strongly in the proportional abundance of cover types and patch aggregation.

Demonstrated quantitative techniques measuring differences in seascape structure provided a starting point to evaluate how spatio-temporal variations in seascape structure may affect biodiversity and ecological processes in these systems.

6.2.3 Theme 2: Ecological relevance of spatial pattern metrics

Due to the biophysical differences between land, shallow (< 30m) and deeper ocean environments (> 30m), knowledge gaps remain on the transferability of the ecological relevance of patch-based metrics to deeper water fish associated with benthic seascapes. To contribute to filling these gaps, patch-based metrics were a key approach used in this thesis to relate the structure of the benthic seascape to the occurrence and distribution of demersal fish on seamounts and mesophotic reefs and for ecological hypothesis testing.

Although spatial pattern metrics proved useful for assessing these biodiversity-environment, relationships, across case studies, site and depth (48% of fish abundance at SWIR seamounts, 38.35% of fish abundance at Seychelles MCEs) were the main parameters influencing broad-scale biological patterns. These site- and depth dependent effects determine the boundary conditions for more local effects of seascape composition, configuration and terrain structure on biodiversity.

Objective 2a: To assess the utility of patch-based metrics quantified from categorical habitat maps to explain and predict biological patterns

Findings from this thesis clearly demonstrated that the character and spatial pattern of seascape patches, proven to be ecologically relevant on land and in shallow-water marine environments (Boström et al., 2011; Hinchey et al., 2008), are also relevant for identifying environmental predictors of fish species occurrence and distribution and

assemblage structure in deep-sea environments. At seamounts, patch-based metrics of seascape structure were the most influential predictors of fish family occurrence and assemblage structure after site and depth. At mesophotic reefs, incorporating fine-scale patch-based metrics increased the amount of variance explained in abundance and biomass by over 10%, and helped distinguish between different fish assemblages. However, for some associations, metric interpretations did not appear to be directly transferable from either terrestrial or shallow water ecology, and specific findings for composition and configuration metrics are discussed below.

Seascape composition

Broad (km) and finer (cm-m) scale variations in seascape composition, measuring the proportional abundance, diversity and size of habitat patches, influenced fish assemblages at both MCEs and seamounts.

The proportional abundance of geomorphological classes and cover types was expected to influence fish assemblages, and indeed was highly relevant in both study systems. At the SWIR seamounts, the proportion of geomorphological classes was the most important predictor of abundance, richness and diversity after site and depth. Specifically, summit and ridge habitat types were more important than slopes and flanks in supporting high fish abundance, richness and diversity. Transects with greater gravel, coral rubble or live coral cover were associated with higher fish abundances than transects dominated by sediment veneer, mud or boulders, confirming an important role for cold-water coral as fish habitat (Auster et al., 2005). For MCE related fish, the relative abundance of substrate types was important in explaining inter-assemblage variations (7.5% abundance, 6.11% for biomass), with distinct patch types associated with 30-60 m (coral, macroalgae/seagrass, sediment) and 120 m (bedrock, sediment veneer) assemblages. Additionally, the number of cover types (substrate richness) was a significant explanatory variable of total abundance of fish.

Larger patch sizes were expected to influence fish abundance positively through larger habitat availability from the perspective of minimum area requirements - also important for conservation planning (Pe'er et al., 2014)-, but, following niche theory,

negatively influence diversity and richness due to reduced seascape heterogeneity (Ismail et al., 2018). At the SWIR seamounts, assemblage diversity decreased with larger patch sizes and the overall abundance of aggregating fish families dependent on large, homogeneous patches associated with the summit. However, responses to patch size varied across individual fish families suggesting taxon-specific effects. This family-specific effect is also found in other study systems (Anderson et al., 2009), and may be explained by the fact that different families can have different functional traits, resulting in different habitat preferences. For MCE fish, no effects of patch area were found, this might be linked to the reduced spatial extent surveyed. Overall, these results indicate a varied effect of patch size, where variations are likely dependent on the biological phenomenon under consideration (Kendall et al., 2011).

Seascape configuration

Across case studies, a range of spatial pattern metrics measuring seascape configuration (i.e. shapes of habitat patches and their physical spatial arrangement) were applied. The main parameters measured were patch and seascape shape, aggregation and division, and interspersion.

More complex patch shapes were expected to negatively influence fish assemblage characteristics due to edge effects, that can increase exposure to external disturbances (Ries & Sisk, 2004). However, results from this thesis show a more nuanced perspective. At the SWIR seamounts, family abundance and richness were, in fact, positively associated with complex patch shapes. Likewise, complex patch shapes supported increased Shannon diversity and richness of MCE fish. Positive effects of increased edge environment on fish have also been found in other seabed environments (Moore et al., 2011) and shallow water environments (Boström et al., 2011). Complex shapes may create a more heterogeneous environment with greater structural diversity (Friedlander & Parrish, 1998), that following niche theory, would be positively related to richness and biological diversity. Additionally, habitats with several patches and more edge effects could support species using multiple habitat types (e.g. shelter between coral, but feeding on sand) (Staveley et al., 2017). Yet, simple patch shapes also

proved important explanatory patterns. Several sediment-associated SWIR fishes (Sebastidae, Scorpaenidae), and MCE fish abundance and biomass in 30-60 m transects were associated with simple patch shapes, which indicates increased availability of homogeneous core habitat. Overall, results indicate that although complex patch shapes have been conceptualised as negative on land, their effects in seabed environments can vary and appear to be taxon-dependent.

In landscape ecology, landscape aggregation, interspersion and patch proximity have been associated with structural connectivity (Turner & Gardner, 2015). Conversely, landscape fragmentation has been conceptualised as having negative effects on biodiversity due to the breaking up of habitat in smaller and separated patches. Results from chapters 3 and 5 show that, like responses to patch shape index, the interpretations of effects are more nuanced in the deep sea. At the SWIR seamounts, measures of seascape aggregation (landscape shape and contagion index) were most important in explaining biological patterns; however, its influence appeared to vary between fish families and the seamount environment under consideration. Summit-associated mesopelagic families were strongly dependent on simple aggregated seascape characteristics, and some flank-associated families linked to seascapes with a higher contagion index. These outcomes suggest the importance of aggregated seascape characteristics, that would be expected to provide structural connectivity. However, larger, continuous habitat may also correspond to older, more stable habitat with diverse biological communities that have had more time to develop. However, bathypelagic families typically showed stronger associations with patchier seascape characteristics, which may provide a more heterogeneous environment with more edge environment. Likewise, for MCE fish, the effects of seascape aggregation and mixing appeared strongly dependent on assemblage type and depth. At 30-60 m, abundance, biomass, diversity and richness increased with clumped and aggregated seascape characteristics. However, for assemblages at 120 m depth, abundance, biomass, richness and diversity appeared to increase with patchier and fragmented habitat characteristics, which offer greater structural diversity (Moore et al., 2011).

Overall, this thesis shows patch-based metrics of composition and configuration are important to explain the occurrence and distribution of deeper fish assemblages, in some cases functioning as the main explanatory variable, and therefore form valuable contributions for applied ecological research and marine spatial planning focusing on the seabed. However, results show that the ecological effect of seascape aggregation, division and intermixing are variable, and resolving these effects requires a subtler interpretation including the biological phenomenon and environment under consideration (Anderson et al., 2009). Additionally, resolving effects of seascape and patch characteristics will require an explicit consideration of scale including determining scale dependency and context dependency (Kendall et al., 2011).

Objective 2b: To advance the application of surface metrics, DMs and their outputs to predict biological patterns and processes

Continuous geomorphological structure, quantified using surface metrics, influences marine species distributions with effects on multiple spatial scales and may also act as a spatial proxy for parameters on which detailed data is unavailable (Brown et al., 2011; Wilson et al., 2007). Case studies in this thesis demonstrated three important applications of surface metrics: 1) to produce geomorphological maps of seamounts, 2) to create spatial predictors for predictive distribution modelling of deeper reefs, and 3) to assess fish-habitat associations at seamounts and MCEs. As habitat maps were produced using established approaches (Ismail et al., 2015; Verfaillie et al., 2009), the main contributions of this thesis to the application of surface metrics lie in the predictive ecological modelling of benthic deeper reef assemblages, and assessing fish-habitat associations at seamounts and MCEs.

For deeper reefs, surface metrics extracted over multiple spatial scales performed as reliable predictors for mapping benthic assemblages. As expected, the occurrence of individual assemblages was related to interacting effects of multiple predictor variables. Across sites, main drivers of mesophotic community occurrence and distribution were depth, substrate characteristics, curvature, slope and habitat complexity, their relative importance influenced by assemblage functional characteristics. Although spatial predictive modelling studies incorporating surface metrics have mainly focused on

mapping species distributions, this study further showed assemblage-level approaches may provide significant advantages by including multiple taxa contributing to the structure and functioning of deeper reefs.

Terrain metrics also proved important in explaining demersal fish occurrence and distribution, especially in MCEs. Quantitative terrain metrics extracted at scales of multiple metres have been applied in MCEs (Osuka et al., 2021; Trembanis et al., 2017; Weijerman et al., 2019), but this study was the first to demonstrate the ecological importance of cm-scale terrain structure in deeper water MCEs. Structurally complex terrain characterised by ridge-like features supported higher fish abundance, diversity and richness across the depth gradient. These areas might be linked to the presence of hard substrate, geomorphological features or complex coral habitat, offering additional niche space for refuge and feeding. Fine-scale structural complexity, which was quantified using SfM photogrammetry, is also a demonstrated predictor of fish assemblages associated with shallow-water and cold-water coral reefs (Ferrari et al., 2016; Price et al., 2019; Storlazzi et al., 2016), and these results confirm for the first time that structural complexity is important for fish assemblages associated with mesophotic reefs. At the SWIR seamounts, structural complexity positively influenced diversity and richness, but only some fish families strongly responded to other terrain characteristics. Variable results of the effect of seafloor complexity and morphology in deep-sea fishes were also found in a review of twenty studies (Borland et al., 2021), and this phenomenon may be explained by the different life-history strategies of studied families.

Overall, results from this thesis demonstrated that structural complexity and curvature of the terrain are reliable explanatory and predictive variables of the occurrence of benthic assemblages and fish in investigated study systems. This will be useful for determining environmental parameters to measure in future studies and when identifying ecologically important areas for biodiversity conservation.

Objective 2c: To assess the utility of combinations of patch-based and terrain metrics to explore the effect of heterogeneity in seascape structure on biodiversity and identify relevant predictor variables

The seabed exhibits multiscale patchiness and gradients in environmental characteristics, that can be measured by patch-based (seascape composition and configuration) and terrain metrics, and are likely ecologically relevant. Case studies in this thesis demonstrated that all categories of seascape metrics (composition, configuration and terrain structure) explain fish-habitat associations, indicating a combined effect of patchiness and continuous variation.

At the SWIR seamounts, patch-based metrics had higher predictive power than terrain derivatives commonly used in developing proxies for deep-water fish biodiversity. In particular, the proportion of summit and ridge habitat, landscape shape and patch shape exerted large effects on fish families and assemblage characteristics. Terrain metrics, primarily structural complexity, also contributed to explaining additional variation, but were less prominent. This may be related to the fact that terrain metrics formed input for the geomorphological class maps from which measures of seascape composition and configuration were calculated and are therefore partly incorporated in these metrics. For the MCE fish, measures of seascape composition, configuration and terrain structure were all statistically significant in explaining variation in species abundance and biomass across clusters. In addition, fine-scale interactions between terrain structure, habitat composition and configuration explained individual assemblage characteristics.

Overall, these results confirm that both categories of metrics (patch-based and terrain) are important in explaining ecological associations, following findings from shallow reefs (Wedding et al., 2019) and have merit for incorporating in ecological analyses of habitat suitability. The importance of predictor variables was strongly dependent on depth and geographic location, limiting the capacity to identify predictor variables relevant across study sites and systems. However, recurring variables across locations and study systems included patch size and shape, contagion, landscape shape, structural complexity and curvature, suggesting applicability of these to other systems.

6.2.4 Theme 3: Supporting applied seabed management research

The seamounts and deeper reefs considered in this thesis are recognised as ecologically important features, that would benefit from evidence-based management action (Marsac et al., 2020; Stefanoudis et al., in review). This thesis demonstrated techniques to obtain spatially explicit knowledge on the multiscale environmental factors influencing the occurrence of biodiversity and habitats and possible priority features for conservation, which can support developing effective management strategies for these and other seabed ecosystems.

Objective 3a: To include multiscale spatial data and geographical context to determine scale dependency and cross-scale interactions on biodiversity characteristics

A multiscale perspective is important to identify and integrate observational, thematic and analytical scales relevant for the ecological phenomenon under consideration and avoid scale mismatches resulting from selecting a single arbitrary focal scale (Wiens, 1989). The importance of scale selection and scale effects for ecological and applied research have been acknowledged throughout the case studies in this thesis, with different methodological approaches applied to select thematic and analytical scales dependent on the primary questions, data characteristics and perceived ecological relevance.

At the SWIR seamounts, the 'Estimation of Scale Parameter' approach (Drăguţ et al., 2010) was used to select the appropriate scale for producing geomorphological class maps representing broad-scale seascape features from data with a fixed observational scale (resolution of 25 m), as has been done in other deep-sea environments (Ismail et al., 2015). Resulting geomorphological class maps were used to study fish associations with seascape heterogeneity in their wider context. The mobility ranges or other traits determining the scale of ecological processes is unknown for most deep-sea species (Levin et al., 2019), therefore selecting appropriate analytical scales is rarely straightforward. Here, analytical scales were determined by using multiscale seascape sample units around each observation and assessing the strength of the relationship between biological observations and seascape characteristics at each scale. In deeper

reefs, multiscale approaches were used to select appropriate analytical scales in the two case studies that varied strongly in observational scale. For both the predictive mapping of benthic assemblages and identifying fish-habitat relationships, predictor variables proved more informative at certain scales, confirming the importance of scale selection and the potential for identifying scale dependency. Additionally, the benthic assemblage predictive modelling study showed that biodiversity responses could vary by predictor variables extracted at different scales, confirming the importance of a multi-scale approach in distribution modelling (Pittman & Brown, 2011).

Case studies did bring possible scale mismatch issues to the fore, which proved relevant for ecological interpretations of obtained results or reduced model predictive power. For example, the geomorphological class maps used in the seamount fish study were not explicitly produced at spatial scales ecologically relevant for the fishes' home range movements (e.g. matching mobility and daily space use), as such knowledge was unknown or highly variable between studied fish families.

At a finer observational resolution (m), models produced to predict the distribution of rariphotic deeper reef assemblages had limited explanatory and predictive power. The species that characterise these assemblages occurred on patches of hard substrate which often occurred interspersed between soft substrate. The spatial resolution at which spatial predictors (2 x 2 m or broader) were extracted likely did not capture substrate variation at the scale influencing the occurrence of species, resulting in a possible analytical scale mismatch. Where thematic and analytical scale may have been too broad for SWIR fish and rariphotic reef assemblages, for some MCE fish it may have been too fine. Although the home ranges of smaller fish might be within the spatial extent of each surveyed transect, many larger-bodied fish will be mobile over extents greatly exceeding the 50 m x 5 m areas covered in this study which may compromise the detection of accurate relationships.

Overall, these case studies demonstrated different methods to explicitly incorporate scale selection considerations at an analytical level to improve ecological interpretations of results. However, ideally ecologically meaningful scale selection is always a consideration when developing a sampling design and mapping strategy. The sampling design

and data used in these projects were not designed specifically for the questions asked, but instead chosen to be reusable for multiple research questions. Further studies using maps and metrics produced at appropriate scales are likely to improve reliability of obtained results, but might limit the applicability of data to answer other questions.

Objective 3b: To apply seascape ecology concepts and analytical techniques to support prioritisation of important habitat for deeper reef ecosystems and seamount communities

Using seascape metrics, this thesis identified several characteristics of seascape structure behind the occurrence and distribution of WIO biodiversity, which were used to identify areas of priority habitat for commercially important fish species.

At the SWIR seamounts, spatial pattern metrics revealed that benthic and demersal seamount-associated fish responded to unique combinations of seascape composition, configuration and terrain structure, with some overlap between families found in the same depth zones. This indicates that, with reference to the SWIR, similar seascape characteristics are important for co-occurring families. Broad-scale habitat features, specifically the summit and the proportion of ridge habitat appeared to be the main drivers of assemblage characteristics which is consistent with results from other regions (González-Irusta et al., 2021; Porteiro et al., 2013). This study demonstrated for the first time that the spatial configuration of patches identified from geomorphological class maps, especially their spatial continuity and shape, are also key drivers of seamount fish assemblage characteristics. Systematic conservation planning efforts aimed at biophysical representation could therefore, in addition to incorporating representative subsets of biophysical features as summit and ridge, benefit from consideration of the spatial configuration of these features. With several conservation initiatives, including in the WIO, focused on focal species (indicators, keystones, umbrellas and flagship species) (Zacharias & Roff, 2001) priority questions include resolving what features matter for individual species. This thesis contributed to these knowledge gaps by specifically identifying habitat preferences for commercially important seamount fish families (orange roughy, oreos, alfonsinos, pelagic armourhead).

In deeper reef ecosystems, spatial pattern metrics proved useful to study biodiversity-environment relationships for epibenthos and fish. As in other regions (Sherman et al., 2019), deeper reef distributions were linked to broad geomorphological features as paleo-shorelines, terraces and other raised features that provide topographically complex habitat and hard substrates for colonisation at suitable depths. Importantly, paleo-shorelines at 120 m depth, likely formed during the Last Glacial Maximum, at the investigated locations were associated with high probability occurrences of lower mesophotic assemblages. The consistency between the results obtained per site despite changing geomorphologies suggests robustness of results and is an indication that similar relationships may hold in other WIO atoll environments. Seascape metrics, applied at multiple scales, also provided key insights into habitat associations of MCE fish. Potential priority areas of MCE fish biodiversity at the locations surveyed include sites with steep slopes and high terrain complexity, matching habitat preferences of benthic assemblages and results from elsewhere in the WIO (Osuka et al., 2021). This is a strong indication that MCE fish and benthos co-occur, and these environments form priority habitat or refuge for mesophotic assemblages within Seychelles. The study further revealed distinct habitat preferences along the depth gradient, with MCE fish associated with 30 m-60 m mesophotic habitat characterised by coral cover and connectivity between different substrate types, and 120 m mesophotic habitats by local habitat heterogeneity.

6.3 Future directions

Research conducted revealed that, although incorporating seascape ecology concepts as spatial pattern metrics for the study of seabed environments is of great merit, knowledge gaps remain in three main areas: the characterisation of spatial heterogeneity, the ecological interpretation of spatial heterogeneity and the application of this knowledge to environmental management (Fig. 6.2). Suggestions for future research based on findings from this thesis are discussed below.

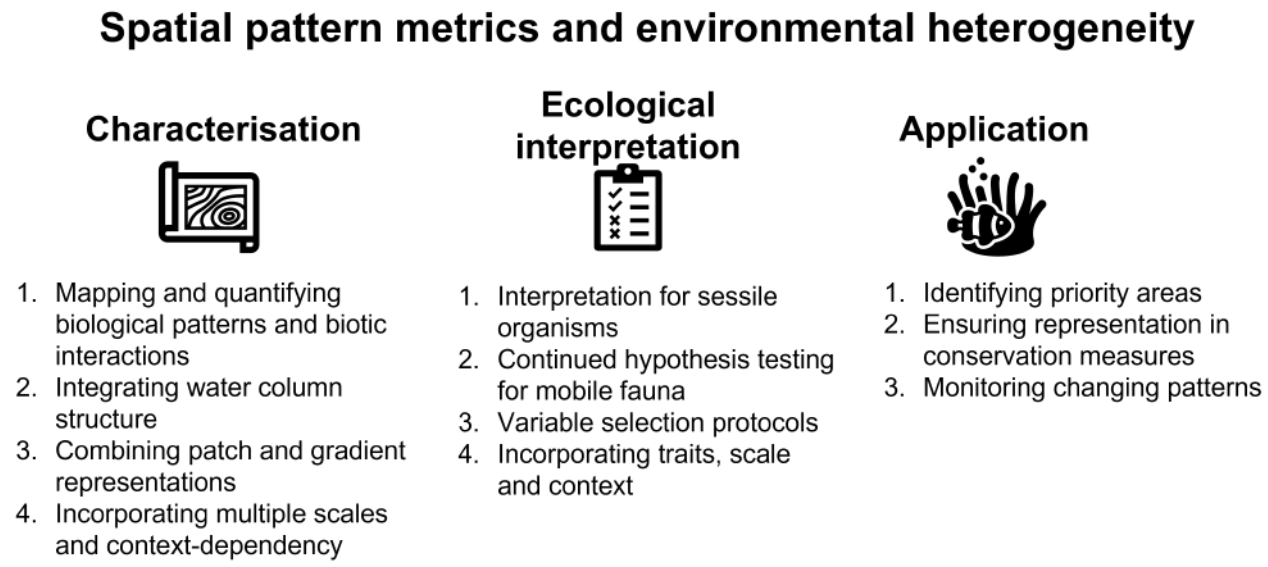


Figure 6.2: Future research areas for the application of spatial pattern metrics at the deep seabed

6.3.1 Characterisation of spatial heterogeneity

Although this thesis primarily focused on spatial patterns of seabed heterogeneity formed by abiotic components as geomorphology and substrate type, seabed heterogeneity is also influenced by variations in multiscale biological and hydrographic parameters that are only partially addressed in this thesis.

Studies of seabed heterogeneity have traditionally focused on mapping abiotic characteristics including geomorphology and substrate type that have subsequently been applied as spatial predictors in ecological models. However, benthic biota such as coral reefs, though often linked to such abiotic characteristics, also form distinct patterns of seabed environmental heterogeneity that do have ecological implications (Quattrini et al., 2012). Unlike on land or in shallow-water environments where such biological patterning (e.g. forest cover, the presence of seagrass meadows) can be mapped using satellite remote sensing, deeper seabed environments require other approaches. The case studies on deeper reefs demonstrated that biological patterns formed by benthic biota on the seabed can be classified from models derived from optical sensors (Ch5) or spatially predicted through distribution modelling (Ch4, Goode et al. 2021). Although not applied in this thesis, produced benthic maps are valuable inputs for further models

incorporating the effect of biologically produced environmental heterogeneity. They may, for example, function as inputs to predict the distribution of other species associated with seabed environments, and research is underway (Dougherty et al., in prep) to link habitat suitability maps in Ch4 to the distribution and occurrence of fish species around Seychelles. Other than representing the occurrence of biological components, there is also great potential for research creating representations of other forms of biological (e.g. predation pressure, dispersal) or anthropogenically produced heterogeneity (e.g. fishing pressure, noise pollution), as these also affect habitat suitability and ecological processes (Bowden et al., 2021; Wisz et al., 2013).

In addition to spatial variation in abiotic and biotic components on the seabed, environmental heterogeneity in the ocean is also heavily influenced by the physical characteristics of the overlying water column (Pearman et al., 2020). Its effects influence nutrient availability and habitat suitability, and with many deep-sea organisms reproducing and colonising new areas through pelagic larvae, also extends to ecological processes as dispersal and connectivity. Although terrain metrics may act as a proxy for local hydrographic conditions (e.g. exposure to prevailing currents and wave dynamics), they are unlikely to capture all ecologically relevant variation in hydrographic conditions and water chemistry that may act at very different scales. As seamounts and atoll slopes are highly dynamic hydrographic environments, in the studies linking fish species to seascape characteristics, the lack of metrics incorporating environmental heterogeneity in the water column is at least partly responsible for reductions in total variance explained. Therefore, there remains a need for developing and incorporating metrics of the spatio-temporal characteristics of the overlying water column in models of seascape structure (Kavanaugh et al., 2016; Sayre et al., 2017), either in 2D (a data layer representing hydrographic characteristics directly above the seabed) or 3D (a model incorporating hydrographic variations throughout the height of the water column). Although presented methods of quantifying, comparing and testing ecological heterogeneity will be applicable to 2D maps, multi-dimensional maps may require a different approach.

Further, in many deep seabed systems, transitions between habitat types are not always clear-cut. Rather than transitions between discrete cover types, transitions in abiotic characteristics are often more gradual which has been recognised by methodologies as fuzzy clustering in seabed mapping (Lucieer & Lucieer, 2009)). Although not covered in the case studies of this thesis, the gradual character of some of these transitions will also have implications for the applicability of patch-based metrics of seascape structure. Another future research area in characterising seascape structure is therefore the development of hybrid metrics combining patch-based and surface metrics that will explicitly take these gradual transitions in habitat types into account (Kågesten et al., 2019; Swanborn et al., 2022).

Finally, it is worth reiterating the critical importance of scale and context for characterising spatial heterogeneity. As what constitutes an appropriate scale is strongly dependent on the question and biological phenomenon under consideration, the production of maps representing spatial heterogeneity ideally occurs with explicit consideration of these factors (Lecours et al., 2015). However, the reality of deep-sea research is that appropriate spatial scales are often unknown, and that it can be challenging to collect multiscale data. Both these challenges were apparent in the studies on the SWIR seamounts. Here, broad-scale geomorphological maps were produced to identify main seascape features, but in reality, fish species under consideration might experience their environments over finer or broader spatial scales. In such cases, future research using hierarchical classification approaches could help reclassify broad-scale entities into finer-scale habitat classes. This also includes a consideration of thematic scale (Strong et al., 2019). Ideally, more deep-water studies would be designed with a nested, multiscale approach supported by the right equipment (e.g. AUVs for finer-scale bathymetric mapping, Robert et al. (2017)) which is becoming increasingly available.

6.3.2 Ecological relevance of spatial heterogeneity

With some of the first studies linking deep sea and deeper reef seabed biota to seabed heterogeneity using spatial pattern metrics at multiple spatial scales, this thesis further revealed a number of future research areas related to the interpretation of spatial

heterogeneity specific to deep-sea biota. First, most interpretations of biodiversity responses to environmental heterogeneity from spatial pattern metrics appeared to be geared towards mobile fauna sampling a broader environment, whereas fewer appeared applicable to sessile fauna. Yet, benthic biota form a significant proporion of seabed ecosystems and therefore resolving the potential implications of variations in seascape structure remains a priority area for these assemblages. Although the interpretation of common composition metrics did appear applicable to these groups through assumptions from niche theory (Harris, 2012) – particular benthic communities will predictably be associated with particular patch types; a larger diversity of patch types will support a larger diversity of communities; and high habitat heterogeneity will positively correlate with biodiversity because of the presence of a larger number of niches – the interpretation of configuration metrics appeared less straightforward. This is likely linked to the fact that rather than interacting with the spatial patterns of seabed and habitat structure for different activities, sessile benthic biota themselves create distinct seascape patterns. Yet, variations in the spatial structure of seascapes is ecologically relevant for benthic macrofauna (Robert et al., 2014), and developing and resolving its ecological relevance for benthic biota therefore remains an important focal area.

However, even for mobile species the interpretation of variations in seascape structure is not directly transferable from concepts developed on land, because of the large biophysical differences between land and sea, and general uncertainties about habitat requirements of the organisms under consideration. Studies in this thesis provided important indications on the applicability of spatial pattern metrics in explaining the occurrence and distribution from deeper reef and seamount fish fauna, but revealed that effects and interpretations varied with the ecological phenomenon, the species or the assemblage under consideration and were not always directly transferable from land. Although this thesis provided important initial contributions, further ecological hypothesis testing will contribute to a body of knowledge on the effect of seascape spatial heterogeneity on mobile species, mediated by broad-scale environmental factors as depth and geographic location. Specifically, there is value in better understanding the effects of the spatial configuration of seascapes (aggregation, fragmentation) on different

mobile biota as these influence how mobile deep-sea species interact and experience their environment. This can also involve the testing of which types of configuration metrics are relevant across systems and employing acoustic telemetry to track movements. This thesis revealed similarity in interpretation and collinearity between many configuration metrics, and therefore further knowledge on the relevance of these metrics will facilitate variable selection procedures. Resolving the ways in which different mobile species interact with characteristics of their environment is a first step towards understanding how important ecological processes as connectivity are influenced by environmental conditions, and therefore which combinations of environmental features should be incorporated in marine management plans. This kind of research would also benefit from incorporating metrics of the overlying water column.

As with the characterisation of spatial heterogeneity, interpreting the ecological relevance of spatial pattern metrics is also strongly dependent on the ecological phenomenon and scale under consideration, and could be negatively affected by scale mismatches. Therefore, future ecological hypothesis testing in these areas will require applying observational and analytical scales that match the ecological requirements (life traits and mobility) of the species under consideration. In particular, hierarchical approaches (Hogg et al., 2016) and incorporating multiscale context (Lecours et al., 2015) are promising strategies to test different analytical scales in extracting measures of terrain structure, seascape composition, and configuration from benthic maps of the area.

6.3.3 Application for applied seabed management research

Awareness of the increasing pressures on seabed ecosystems, many of which are found in the high seas, or areas beyond national jurisdiction (ABNJs), has prompted negotiations for international policy instruments to increase knowledge on deep-sea life (e.g. through SDG14, Life Below Water) and conservation and sustainable use of marine biodiversity in ABNJs (Wright et al., 2018) emphasising marine spatial planning (Wright et al., 2021). Implementing ecosystem-based place- or area-based management tools (ABMTs) as MPAs and zonation to regulate the type and intensity of human activities impacting

seabed ecosystems requires spatially explicit data on ecologically relevant seascape features. the availability of bathymetry data of the global ocean, including in ABNJs, from which biophysical habitat maps can be produced is increasing, sparked by initiatives as Seabed 2030 and the UN Decade of Ocean Science (Ryabinin et al., 2019; Wölfl et al., 2019) including in the WIO (Gates et al., 2021). As discussed in Ch1, seascape ecology has potential for supporting applied seabed management research through identifying areas of particular importance for biodiversity conservation. Although providing practicable conservation advice is out of the scope of this thesis, specifically because no socio-economic data was considered, it did uncover several topics around the relevance of spatial heterogeneity for spatial conservation management of seabed systems that could be explored in future research. The next sections focus on the identification, prioritisation and monitoring of ecologically important areas.

Identification

Ecosystem-based management approaches require information on spatial characteristics of seascapes that are central to landscape and seascape ecology, including the type, diversity, size and shape of areas prioritised for conservation; the distance between them; ecological connectivity and the implications of seascape structure and context (Foley et al., 2010; Pittman et al., 2021). Identifying ecologically relevant seascape features and their spatial arrangement for target species or habitats is important, as the capacity to sample and survey seabed environments limits extensive biological analysis throughout the global ocean and particularly in deep-sea ecosystems and ABNJs (Levin et al., 2019; Wright et al., 2021).

Spatial pattern metrics applied to seabed maps help enable quantitative descriptions and comparisons of seascape composition and configuration across seascapes. Such quantitative descriptions may act as an ecological proxy, help identify target areas for more detailed biological surveys and help test the ecological importance of the size and diversity of features and their spatial arrangement and effectiveness of reserves (Huntington et al., 2010).

Further research to enable the use of spatial heterogeneity, represented in habitat maps as an ecological proxy through considering seascape composition and configuration, is particularly valuable for countries with limited research budgets and/or large marine territories, such as Seychelles, and in ABNJs where extensive ecological data is lacking.

Prioritisation

By visualising the distribution and occurrence of biophysical patterns, habitat maps and spatial pattern metrics could provide an important decision support tool for marine managers to investigate possible priority features for incorporating into conservation and management strategies. When prioritising seabed areas for inclusion, an important consideration is the concept of representation: ensuring that a representative subset of the diversity of biophysical conditions is included (McQuaid et al., 2020; Wedding et al., 2013). This is most commonly interpreted as representation of broad-scale features (seamounts, banks, ridges) and biophysical gradients. Knowledge of the diversity of ecologically important habitat features is an important starting point for marine managers for possible target locations for area-based management tools, but this thesis confirmed that the spatial arrangement of seascape features also merits consideration when designing MPAs or protected area networks.

This thesis showed that the same biophysical features (seamounts) can exhibit spatial variation in habitat characteristics within and amongst them, which likely has ecological implications. Therefore, when possible, the spatial characteristics of the seascapes of individual features considered for protection (e.g. seascape aggregation, fragmentation and interspersion) will be relevant to incorporate in considerations of representation. Over broader scales, the spatial arrangement between habitats and regions influences connectivity, relevant for assessments of how target systems depend on and support surrounding areas and when designing networks for management (Balbar & Metaxas, 2019). This is particularly pertinent in the WIO, as its coral reefs and seamounts are highly connected to surrounding areas through currents and larval dispersal (Crochelet et al., 2020; Maina et al., 2020). Additionally, many species important to conservation in the region, including sharks, pelagic fish species and

turtles, are highly migratory and will use spatially dispersed habitats. The further development of measures of heterogeneity in the overlying water column is also a priority area to support considerations of connectivity.

Monitoring

Seascapes are variable over space and time, and effective assessment of seabed ecosystem change, including under human impact, requires monitoring (Howell et al., 2020). This thesis demonstrated that spatial pattern metrics can help quantifying and comparing seascape structure, which has value for such monitoring programs to assess spatio-temporal changes in seascapes and community structure. As time-series monitoring of sites is rare in deep-sea environments, monitoring applications of spatial pattern metrics are currently most viable for comparisons between sites.

However, with time-series monitoring recognised as a priority for deep-sea research and initiatives as the Global Ocean Observing System and the Deep-Ocean Observing Strategy (DOOS) (Levin et al., 2019), spatial pattern metrics will likely become more relevant to assess how the composition and configuration of seascapes and the spatial characteristics of associated communities (Teixidó et al., 2007) change over time. Further, recognising that pressures on seabed environments continue to increase, spatial pattern metrics have potential within environmental impact assessments to understand how anthropogenic (e.g. trawling, seabed mining, offshore construction) or natural disturbances have or might impact seascape spatial structure. This is particularly pertinent for the BBNJ negotiations and discussions at the ISA.

6.4 Conclusion

This thesis demonstrated that seascape ecology offers a conceptual framework and analytical techniques to quantify and interpret multiscale seascape spatial structure at the level of individual patch types and seascapes. Spatial pattern metrics were applied to quantify and compare seascape structure and functioned as predictors for the occurrence and distribution of benthic assemblages and demersal fish at deeper reefs and seamounts in the Indian Ocean. Ultimately, spatial pattern metrics facilitated a better

understanding of the linkages between seascape characteristics and biodiversity, which has implications for ecology, ecosystem-based fisheries management and biodiversity conservation. The applicability to widely varying study systems suggests spatial pattern metrics are also valuable for studies in other regions and over different spatial scales.

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Appendices

A Appendices to Chapter 2

A.1 Maps of individual seamounts

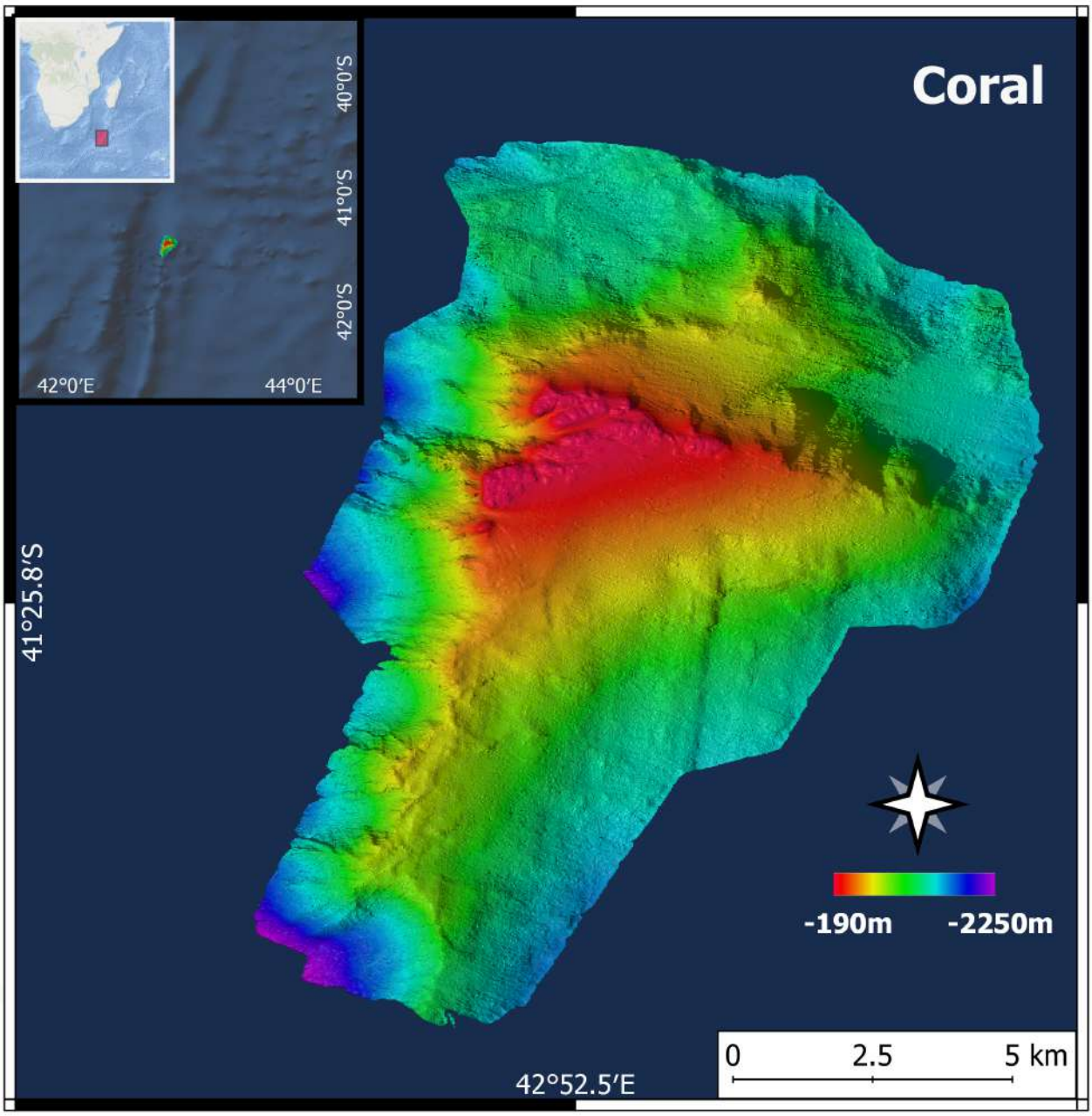


Figure A.1.1: Detailed map of Coral

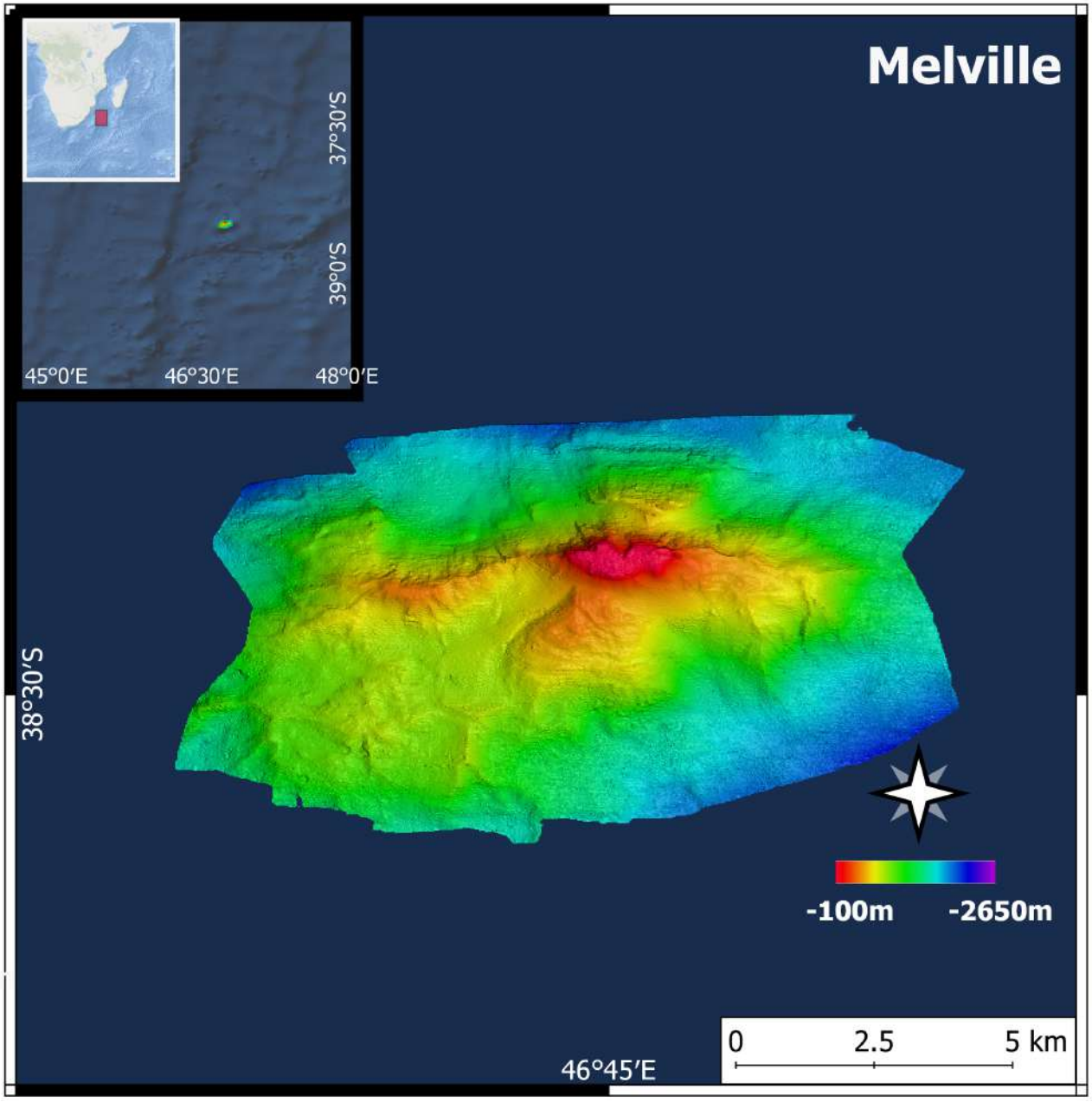


Figure A.1.2: Detailed map of Melville

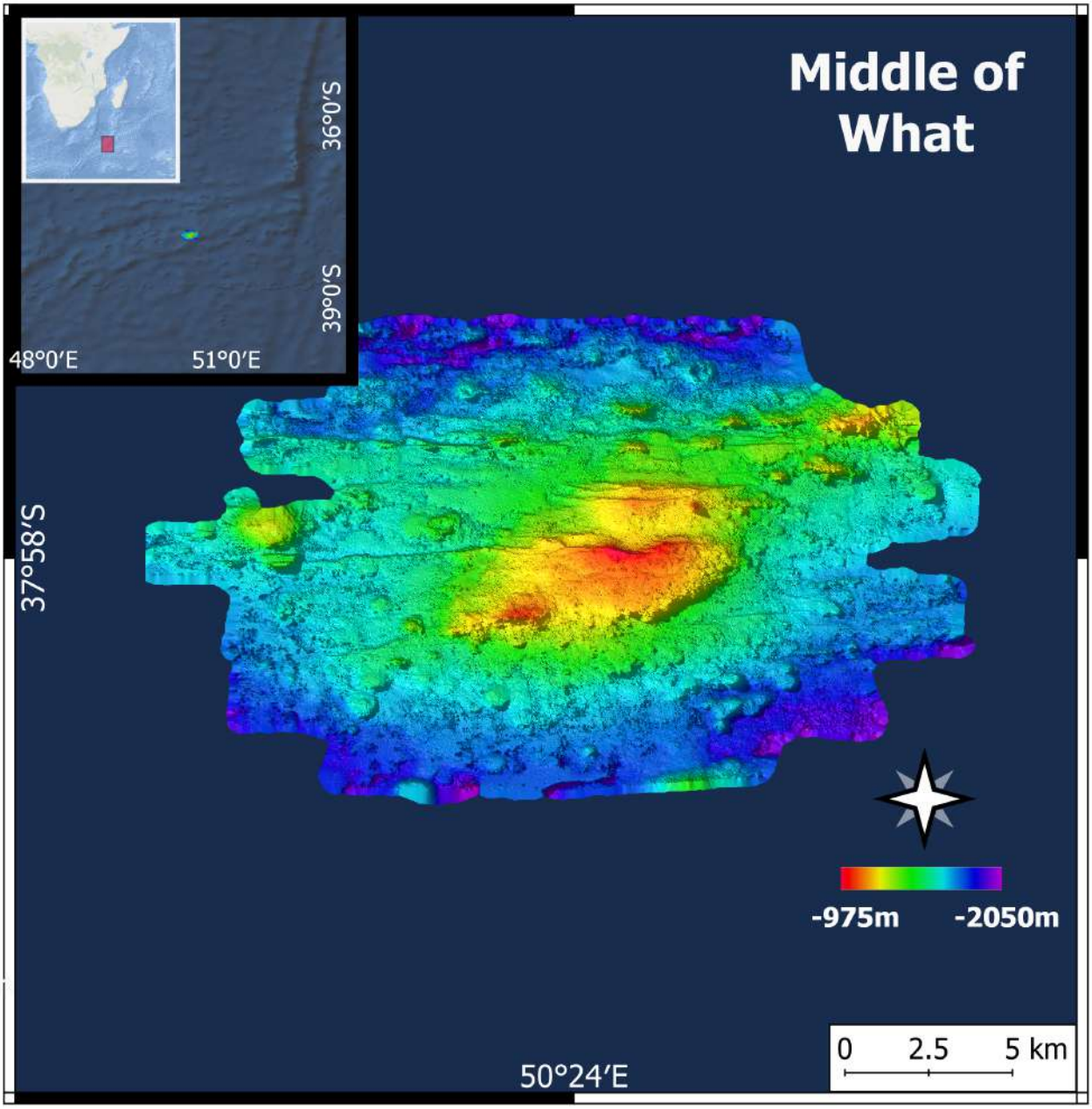


Figure A.1.3: Detailed map of MOW

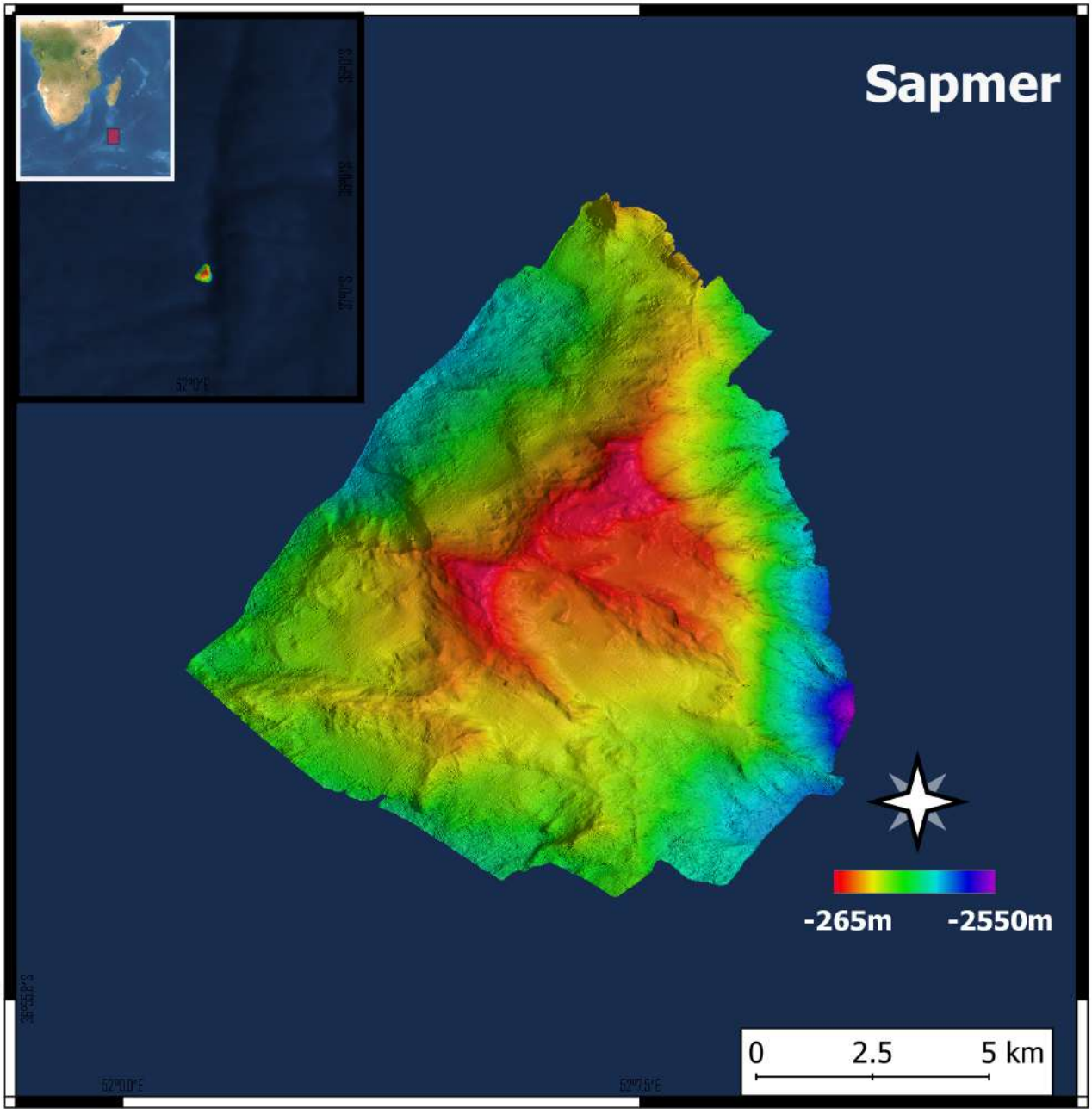


Figure A.1.4: Detailed map of Sapmer

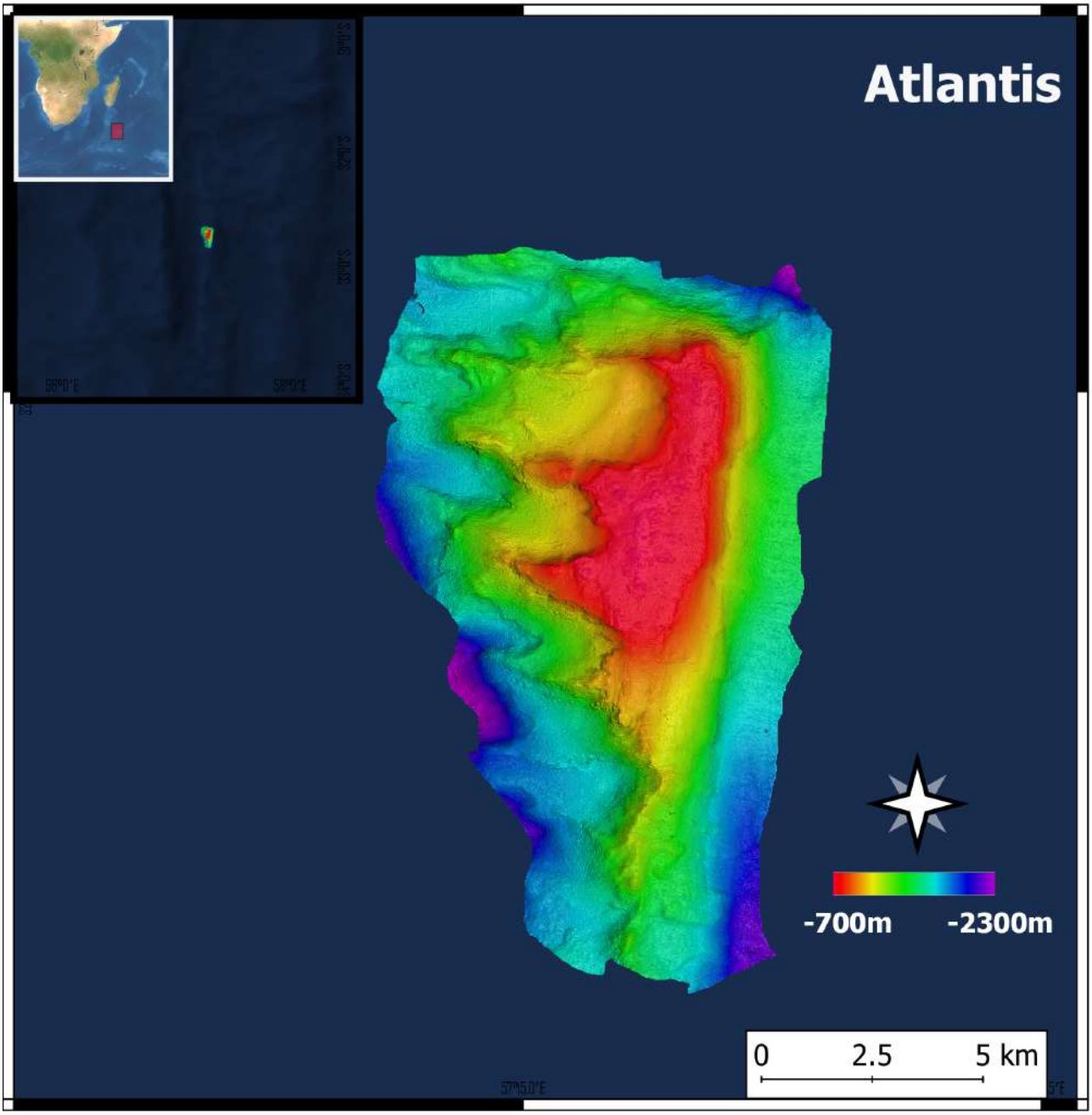


Figure A.1.5: Detailed map of Atlantis

A.2 Backscatter data

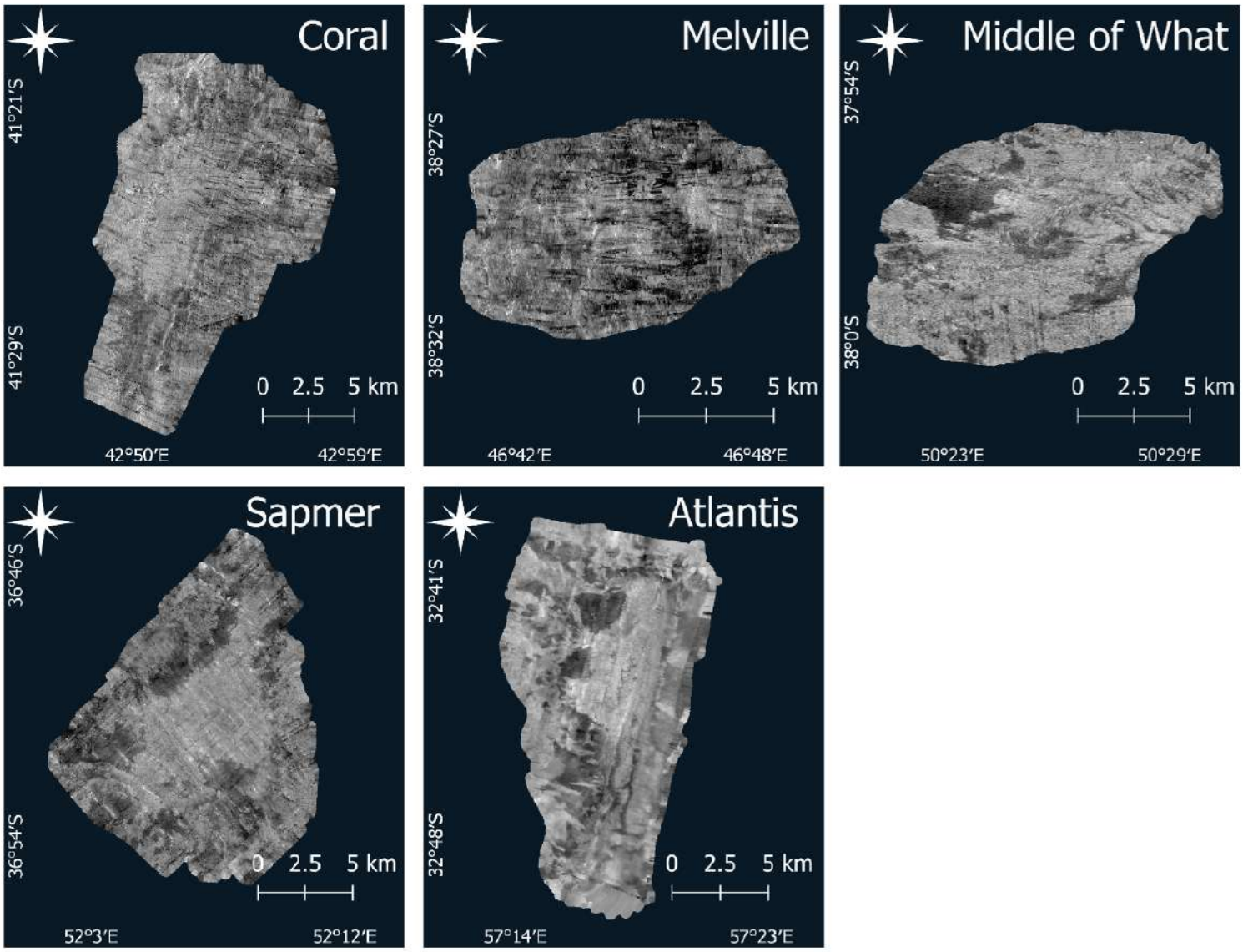


Figure A.2.1: Backscatter images per site

A.3 ROC LV curves

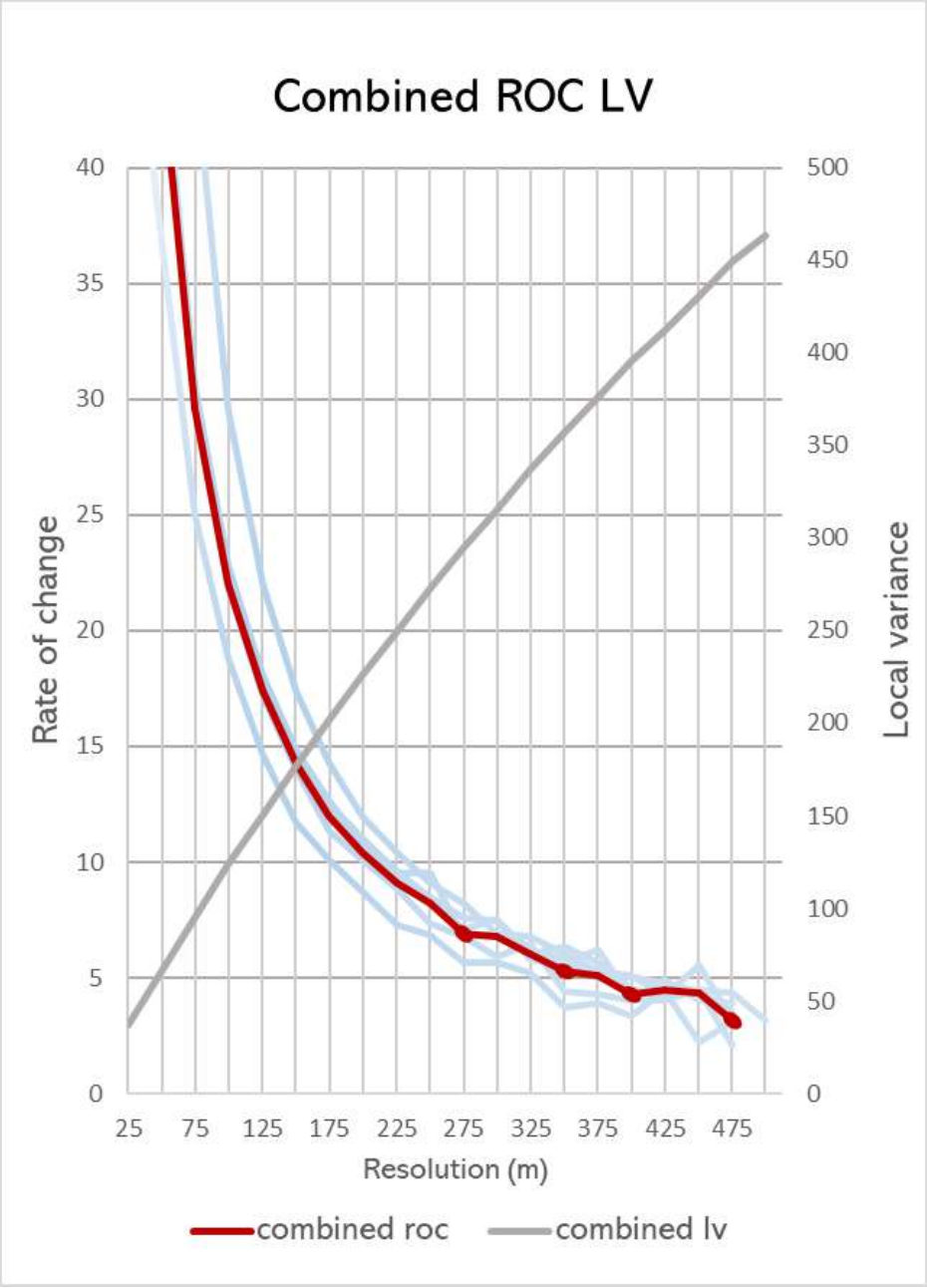


Figure A.3.1: ROC LV curves for scale selection. Light blue shows individual curves per site, red line shows combined curve with first break at 275m resolution.

A.4 Elbowplots

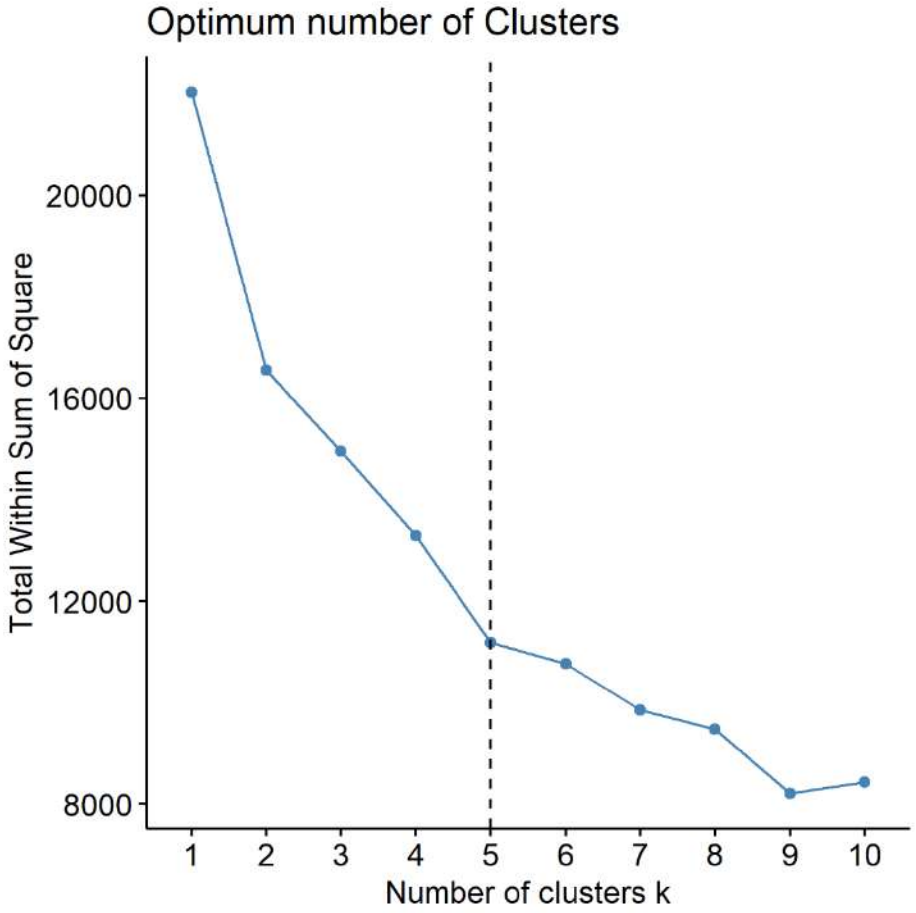


Figure A.4.1: Elbowplot showing a break in curve gradient at 5 clusters, selected as asppropriate number of clusters for the unsupervised K-means classification

A.5 PCA outputs

Table A.5.1: *Significance of axes of abundance (a) and biomass (b) models. The first six axes have a significant (P < 0.05) influence on the model and eigenvalues > 1.*

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Standard deviation	2.019	1.549	1.434	1.377	1.360	1.313	1.220	1.172	1.069
Proportion of variance	0.203	0.120	0.103	0.095	0.092	0.086	0.074	0.069	0.057
Cumulative proportion	0.204	0.324	0.427	0.521	0.614	0.701	0.775	0.843	0.901

Table A.5.2: *Multiscale variable contributions to 9 retained principal components, with key contributing variables (> 0.3 or < -0.3) in bold*

Predictor	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Depth	0.101	0.396	-0.208	**-0.321**	0.155	**0.315**	-0.113	0.106	0.101
Depth br	0.102	**0.392**	-0.209	**-0.319**	0.168	**0.318**	-0.114	0.107	0.102
Backscatter	0.023	0.231	-0.284	-0.147	0.066	**-0.485**	0.279	-0.122	0.023
Backscatter br	0.034	0.254	**-0.301**	-0.141	0.079	**-0.469**	0.262	-0.101	0.034
Curvature	-0.006	0.089	-0.009	-0.217	**-0.665**	0.023	-0.007	0.011	-0.006
Curvature br	-0.032	**0.456**	0.292	0.254	-0.024	0.026	-0.063	**-0.353**	-0.032
Curvature br	-0.032	**0.456**	0.292	0.254	-0.024	0.026	-0.063	**-0.353**	-0.032
Eastness	0.033	-0.038	**0.435**	**-0.341**	0.095	0.068	**0.424**	-0.022	0.033
Eastness br	0.038	-0.041	**0.443**	**-0.350**	0.097	0.056	**0.401**	-0.017	0.038
Northness	-0.134	-0.006	-0.259	0.243	-0.070	**0.352**	**0.474**	-0.093	-0.134
Northness br	-0.151	0.001	-0.275	0.248	-0.069	**0.350**	**0.446**	-0.084	-0.151
Slope	**-0.434**	0.005	-0.012	-0.146	0.060	0.002	-0.085	-0.067	**-0.434**
Slope br	**-0.427**	-0.006	-0.009	-0.162	0.076	0.082	-0.095	-0.022	**-0.427**
Slope of slope	-0.268	-0.032	0.015	0.046	-0.043	-0.180	0.025	-0.041	-0.268
Slope of slope br	-0.135	0.207	0.098	0.171	-0.016	-0.094	0.129	**0.641**	-0.135
TPI	-0.008	0.097	-0.008	-0.215	**-0.665**	0.019	-0.006	0.010	-0.008
TPI br	-0.032	**0.455**	0.292	0.254	-0.024	0.026	-0.063	-0.356	-0.032
TRI	**-0.447**	-0.004	-0.004	-0.120	0.041	-0.034	-0.071	-0.072	**-0.447**
TRI br	**-0.431**	0.009	-0.003	-0.153	0.075	0.078	-0.089	-0.006	**-0.431**
VRM	-0.267	0.014	0.009	0.027	-0.067	-0.167	0.027	-0.012	-0.267
VRM br	-0.122	**0.302**	0.182	0.234	-0.026	-0.079	0.085	**0.511**	-0.122

A.6 Class and landscape metric values

Table A.6.1: Class metrics extracted per habitat class across seamounts. Highlighted values indicate important differences compared to other sites or habitat types

Metric class	Habitat type	Coral	Melville	MOW	Sapmer	Atlantis
Percentage of Landscape	1 (Summit)	10.3448	10.5144	16.4424	14.613	**18.791**
	2 (Slope)	14.97	**26.78**	**5.41**	14.51	21.73
	3 (SE)	26.12	20.73	25.66	**14.11**	23.51
	4 (NW)	**9.42**	15.34	23.84	19.43	**34.54**
	5 (Ridges)	0.79	**1.71**	0.64	0.95	1.43
Patch Area	1 (summit)	5.95	2.57	3.30	8.56	6.59
	2 (slope)	5.22	6.49	**1.28**	3.98	4.81
	3 (SE)	**7.20**	4.36	2.78	3.05	3.76
	4 (NW)	1.82	3.46	2.19	4.71	**4.97**
	5 (ridges)	1.26	1.49	1.01	1.02	1.34
Gyration (Area-Weighted Mean)	1 (summit)	2244.79	764.02	**1965.14**	2244.92	2247.16
	2 (slope)	1914.62	1955.60	**351.68**	2193.26	2742.64
	3 (SE)	3128.18	2438.94	3340.14	**1547.07**	3373.16
	4 (NW)	775.30	764.47	**2992.73**	1864.62	2064.03
	5 (ridges)	331.49	**532.67**	246.03	265.62	295.47
Shape Index	1 (summit)	1.18	1.21	1.22	1.27	1.23
	2 (slope)	1.24	1.27	1.28	1.27	1.26
	3 (SE)	1.19	1.24	1.23	1.28	1.21
	4 (NW)	1.22	1.28	1.21	1.28	1.21
	5 (ridges)	**1.89**	**1.86**	**1.72**	**1.76**	**2.00**
Contiguity index	1 (summit)	0.11	0.15	0.13	0.15	0.15
	2 (slope)	0.22	0.22	**0.24**	0.22	0.22
	3 (SE)	0.12	**0.15**	0.11	0.12	0.12
	4 (NW)	0.12	**0.15**	0.11	0.12	0.12
	5 (ridges)	0.20	0.18	0.16	0.17	**0.22**
Euclidean nearest neighbour (mean)	1 (summit)	78.05	73.63	72.24	75.58	**79.81**
	2 (slope)	87.53	71.92	**89.31**	87.66	82.20
	3 (SE)	74.26	71.13	**66.61**	76.43	**79.44**
	4 (NW)	78.98	**82.24**	**69.43**	77.55	71.46
	55 (ridges)	206.81	210.94	**325.34**	257.10	261.24
ENN coefficient of variation	1 (summit)	0.22	**0.29**	0.25	0.27	0.27
	2 (slope)	0.26	**0.33**	0.27	0.27	0.28
	3 (SE)	0.23	**0.29**	0.25	0.25	0.23
	4 (NW)	0.24	0.26	0.23	0.23	0.26
	5 (ridges)	0.07	0.08	0.05	0.06	0.06
Number of patches	1 (summit)	511.00	419.00	**842.00**	456.00	449.00
	2 (slope)	449.00	**422.00**	716.00	974.00	711.00
	3 (SE)	1066.00	**486.00**	1557.00	1234.00	984.00
	4 (NW)	1522.00	**453.00**	1837.00	1101.00	1094.00
	5 (ridges)	185.00	118.00	107.00	248.00	168.00
Splitting index	1 (summit)	105.39	340.86	47.62	56.77	34.91

	2 (slope)	141.53	37.01	**10688.73**	115.54	74.79
	3 (SE)	26.37	33.90	26.50	**124.25**	28.10
	4 (NW)	**791.08**	251.57	**25.79**	67.86	22.47
	5 (ridges)	**662946.80**	**34655.45**	**790071.30**	**692364.30**	**281471.40**
Clumpiness index	1 (summit)	0.93	0.84	0.88	0.92	0.93
	2 (slope)	0.88	0.86	0.72	0.86	0.85
	3 (SE)	0.91	0.86	0.79	0.82	0.86
	4 (NW)	0.80	0.83	0.75	0.86	0.84
	5 (ridges)	**0.49**	**0.52**	**0.50**	**0.48**	**0.49**
Interspersion and juxtaposition index	1 (summit)	80.51	**95.98**	86.53	97.02	95.57
	2 (slope)	85.34	93.50	90.39	89.29	79.60
	3 (SE)	84.22	87.50	**55.39**	77.24	73.63
	4 (NW)	72.21	**83.87**	**65.65**	79.95	82.30
	5 (ridges)	87.65	86.41	92.92	90.53	93.94
Normalised landscape shape index	1 (summit)	**0.06**	**0.14**	**0.10**	**0.07**	**0.06**
	2 (slope)	0.10	0.10	**0.26**	0.12	0.12
	3 (SE)	0.07	0.11	**0.16**	0.15	0.10
	4 (NW)	0.18	0.15	**0.19**	0.11	0.10
	5 (ridges)	**0.51**	**0.47**	**0.49**	**0.51**	**0.50**

Table A.6.2: *Landscape-level comparison in terms of composition and configuration. Highlighted values indicate important differences compared to other sites*

Metric class	**Coral**	**Melville**	**Middle of What**	**Sapmer**	**Atlantis**
Patch size	**2657.18**	**864.4**	1100.52	2059.58	1922.72
Gyration	2289.98	**1646.30**	**2659.12**	1932.60	2528.47
Shannon diversity	1.35	1.41	1.31	1.43	1.41
Shannon evenness	0.84	0.88	0.81	0.89	0.88
Shape index	8.79	**8.07**	**17.62**	10.84	10.08
Contiguity index	0.89	0.85	0.82	0.87	0.88
Euclidean Nearest Neighbour (mean)	85.12	83.20	**77.26**	90.53	86.47
CV ENN	**121.32**	101.88	**97.5**	117.91	116.62
Number of patches	4127	**1898**	**5059**	4013	3406
Patch density	22.70	24.71	**29.94**	23.63	**21.63**
Splitting index	17.94	15.76	10.25	**20.38**	**8.19**
Contagion index	**45.23**	**39.59**	40.70	40.03	42.27
Landscape Shape index	27.58	**23.76**	32.13	32.61	27.58
Interspersion and juxtaposition index	83.50	**90.78**	**70.97**	85.78	83.41

A.7 Pairwise comparisons

Table A.7.1: *Adjusted p-values for pair-wise comparisons in values of different class metrics per habitat class. Bold values indicate significant (p<0.05) differences.*

	Perc	PA	Gyr	Shape	Contig	ENN	ENN cv	NP	SPLIT	CLUM	IJI	LSI
Ridge - NW	**0.00**	0.25	0.07	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.54	**0.00**	0.06	**0.00**
Ridge - SE	**0.00**	0.07	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.92	**0.00**	**0.04**	**0.00**
Ridge - Slope	**0.01**	0.05	0.04	**0.00**	0.28	**0.02**	**0.00**	**0.04**	0.63	**0.00**	0.97	**0.00**
Ridge - Summit	**0.03**	**0.01**	**0.03**	**0.00**	**0.01**	**0.00**	**0.00**	0.17	0.47	**0.00**	1.00	**0.00**
Summit - Slope	0.96	0.85	1.00	0.96	**0.00**	0.42	0.20	0.93	1.00	**0.03**	0.92	0.18
Summit - NW	0.48	0.35	0.99	0.64	0.42	1.00	0.58	**0.00**	1.00	**0.00**	**0.04**	0.10
Summit - SE	0.28	0.79	0.39	0.96	0.42	0.80	0.90	**0.02**	0.91	**0.06**	**0.02**	0.60
Slope - NW	0.64	1.00	0.32	1.00	**0.00**	0.07	**0.04**	0.11	0.97	0.99	0.12	0.90
Slope - SE	0.85	0.89	1.00	0.95	**0.00**	0.02	**0.01**	**0.02**	1.00	0.96	0.17	1.00
SE - NW	0.99	0.93	0.21	0.95	1.00	0.89	0.97	0.90	0.94	0.61	1.00	0.75

B Appendices to Chapter 3

B.1 Data Preparation

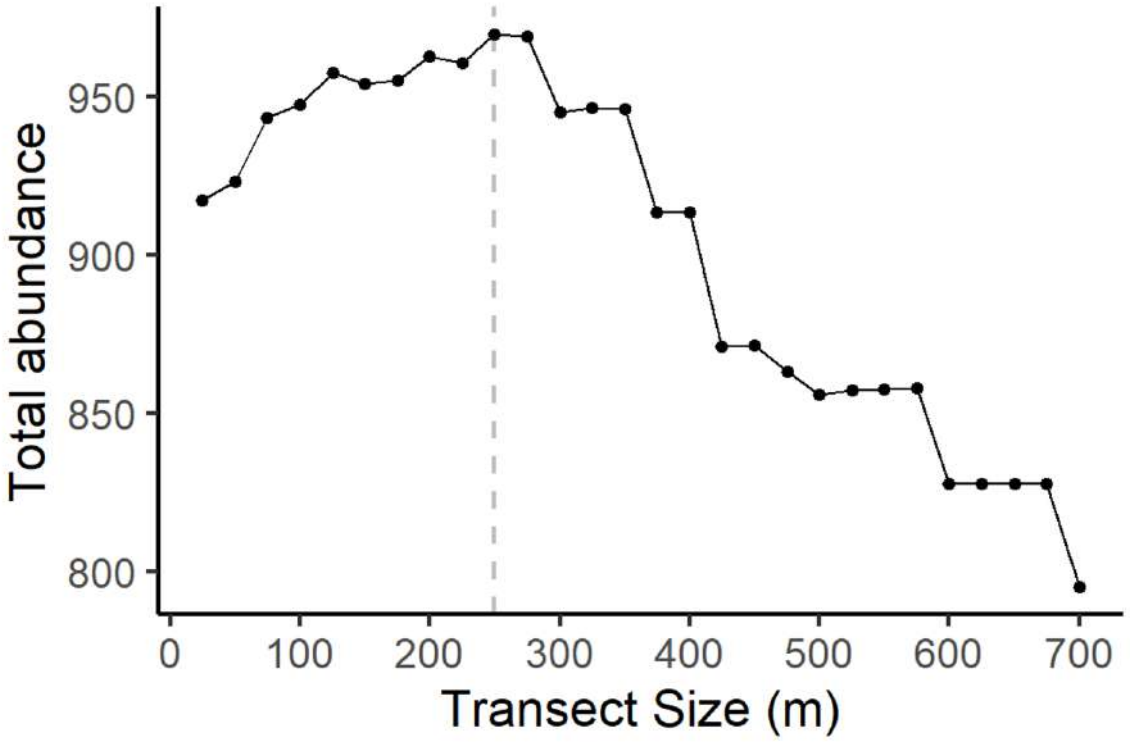


Figure B.1.1: Optimum transect size selection showing that a transect size of 250 m maximizes the total number of observations that can be incorporated in analysis under specified constraints

B.2 Full PERMANOVA results

Table B.2.1: *PERMANOVA indicating that site and depth class had a significant effect on community structure.*

	Df	Sum of Squares	R2	Pr(>F)
Site	2	5.55	0.40	0.001***
Depth class	2	1.05	0.08	0.001***
Site:depth class	1	1.16	0.08	0.001***
Residual	49	6.00	0.44	
Total	54	13.75	1	

Table B.2.2: *Pairwise comparisons between sites, illustrating that all sites differed significantly from each other with the strongest differences between Coral and Atlantis.*

	Df	Sum of Squares	R2	Pr(>F)
Coral vs Melville	1	2.76	0.359	0.003*
Coral vs Atlantis	1	2.68	0.372	0.003*
Melville vs Atlantis	1	1.87	0.292	0.003*

Table B.2.3: *Pairwise comparisons between depth zones, illustrating a significant difference in community characteristics between all depth zones apart from the bathypelagic and mesopelagic.*

	Df	Sum of Squares	R2	Pr(>F)
Bathypelagic vs Mesopelagic	1	0.55	0.045	0.161
Bathypelagic vs Epipelagic	1	1.33	0.376	0.001*
Mesopelagic vs Epipelagic	1	1.17	0.106	0.001*

B.3 Variable interactions for Random Forests

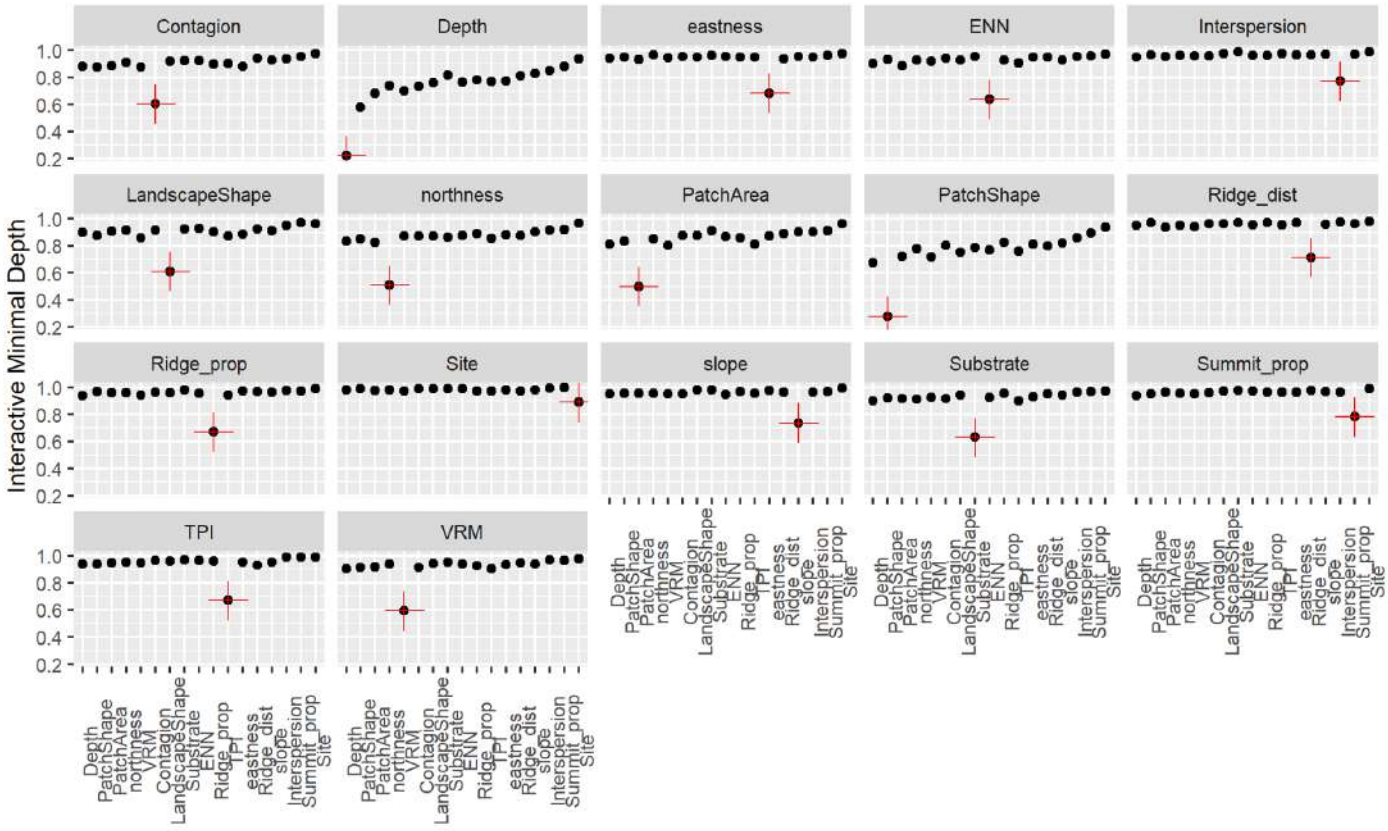


Figure B.3.1: Variable interaction plot for Random Forest model of abundance. Lower values of variable combinations can be indicative of an interaction effect, and were seen for combinations of Depth, Patch Shape, Patch Area and VRM (more complex patch shapes and higher terrain complexity at shallower depths, simpler landscape shapes with larger patch areas and more extended patch shapes).

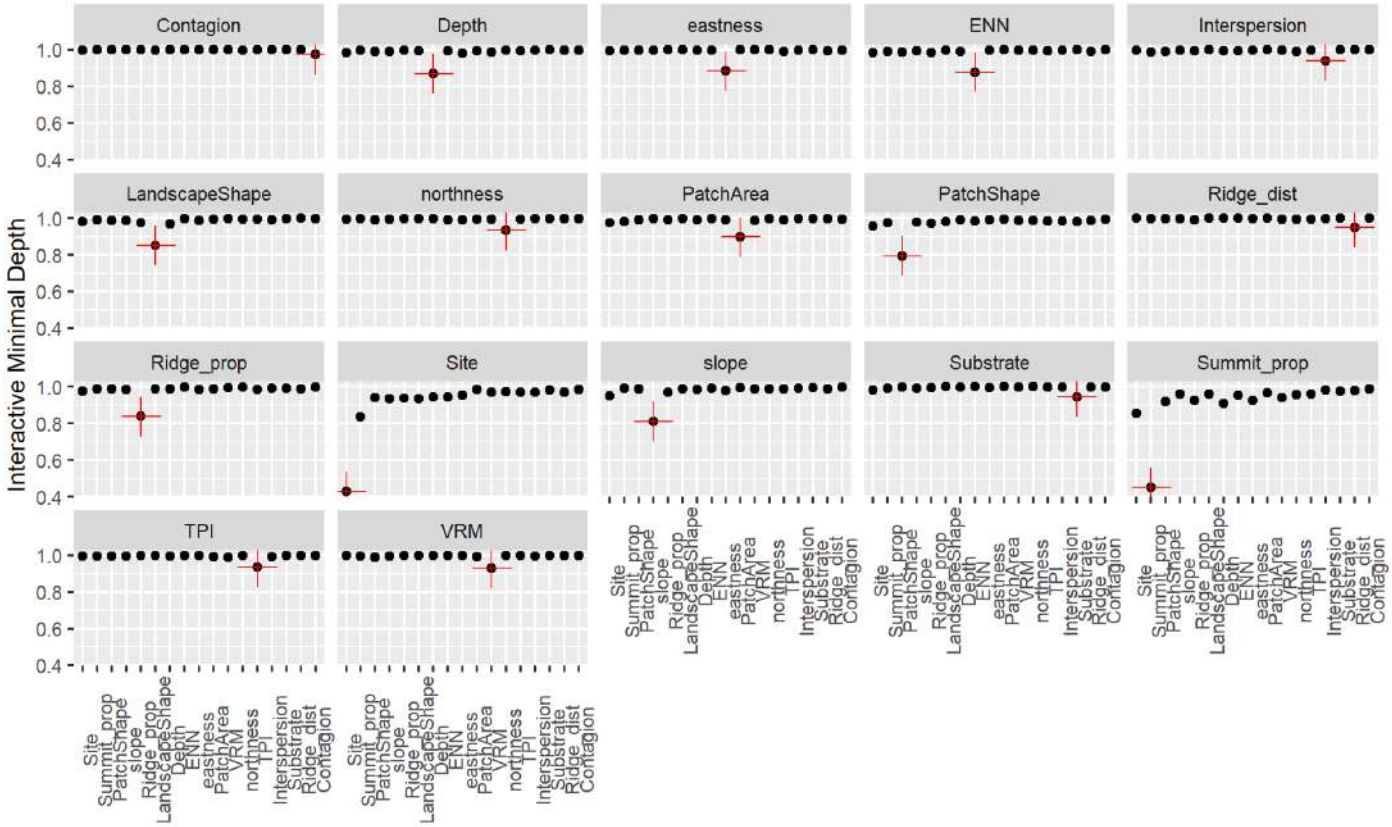


Figure B.3.2: Interaction plots for richness. There were no clear interaction effects, although interactive minimal depth was lower for Site and the proportion of summit.

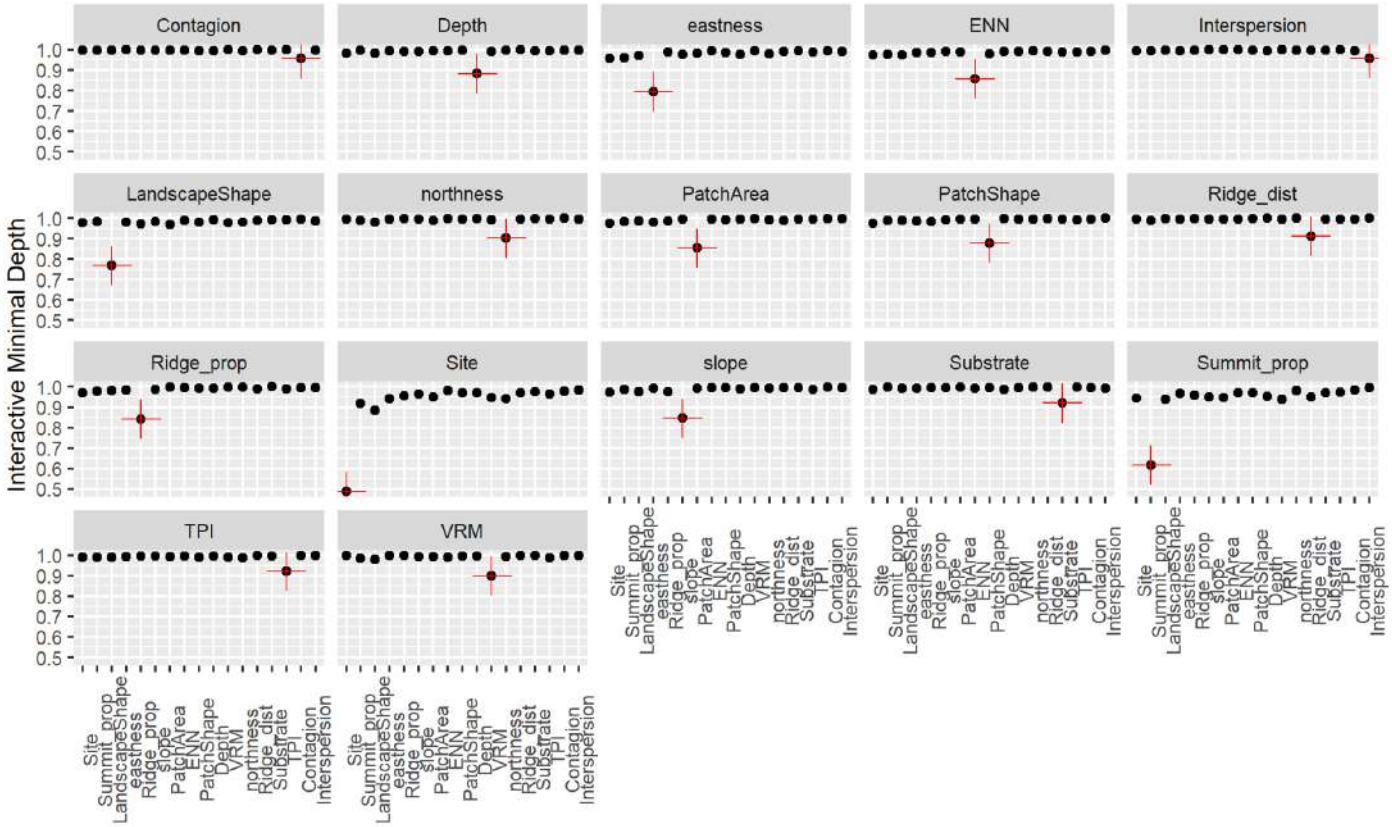


Figure B.3.3: Variable interaction plots for variables included in the random forest models for diversity. Some evidence of variable interactions were observed for Site and Landscape Shape (simpler landscape shapes at Atlantis).

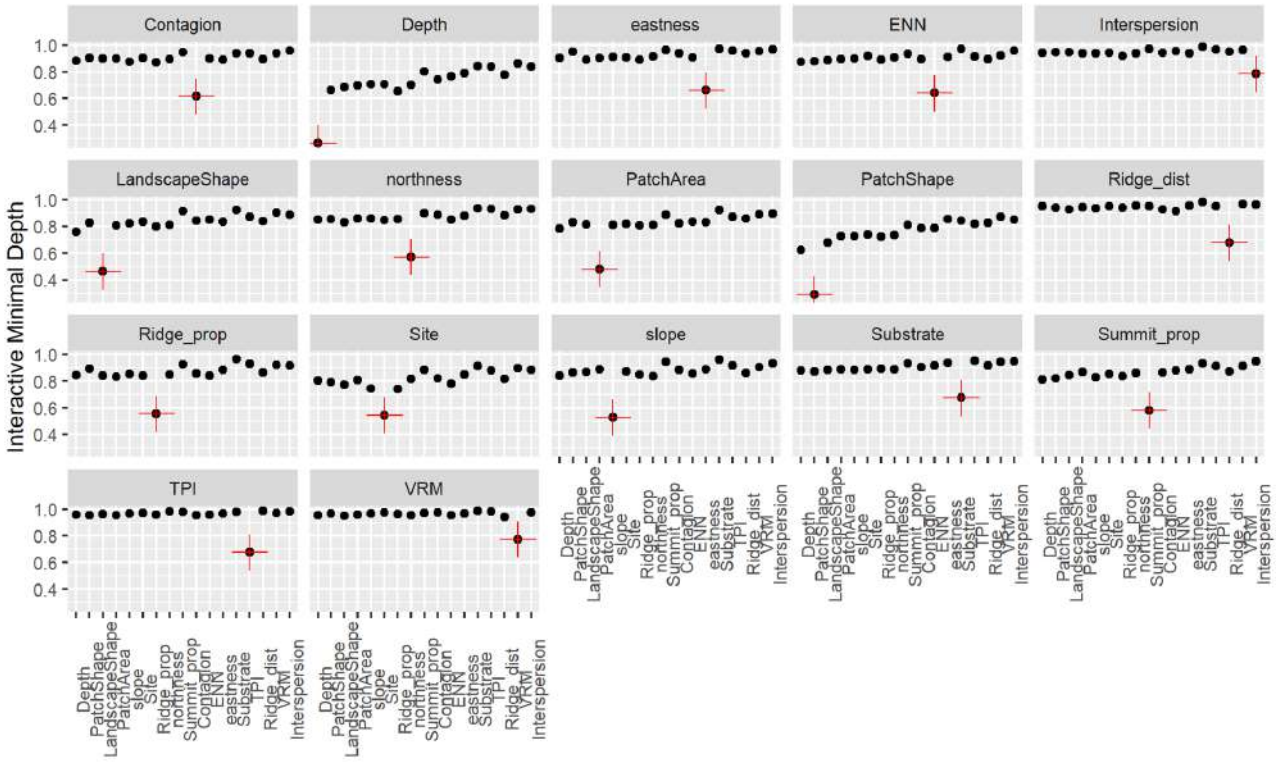


Figure B.3.4: Variable interaction plots for variables included in the Multivariate Random Forests. Low values for variable combinations are indicative of an interaction effect. Some indication of interactions were found for combinations of Depth and Patch Shape (patch shape complexity decreased with depth), Depth and Landscape Shape (landscape complexity decreased with depth),and Patch Shape and Landscape Shape (more complex landscape shapes equalled more complex patch shapes).

B.4 Variable importances and partial dependence plots

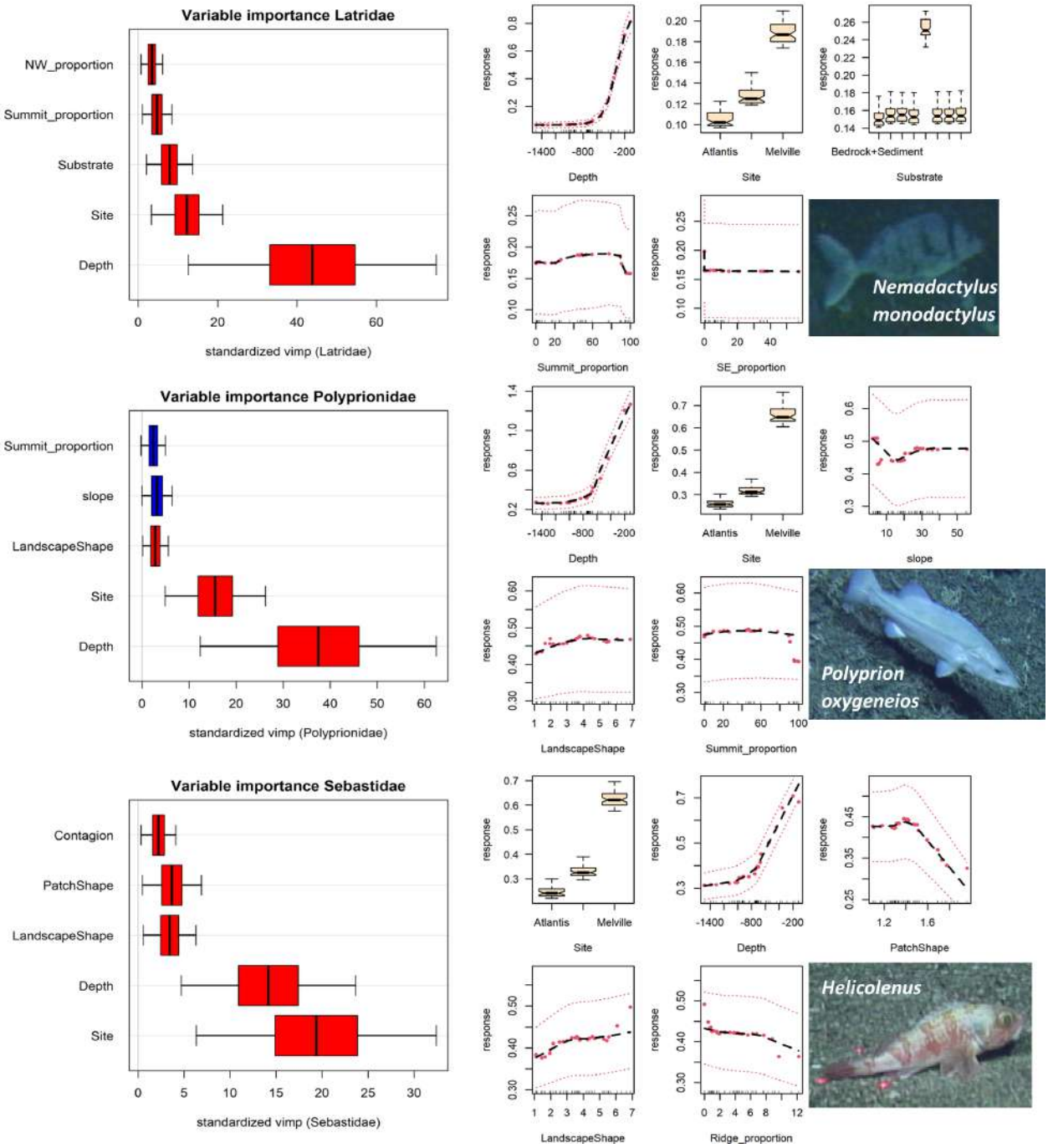


Figure B.4.1: Variable importances epipelagic. Blue indicates non significant (P<0.05) effect.

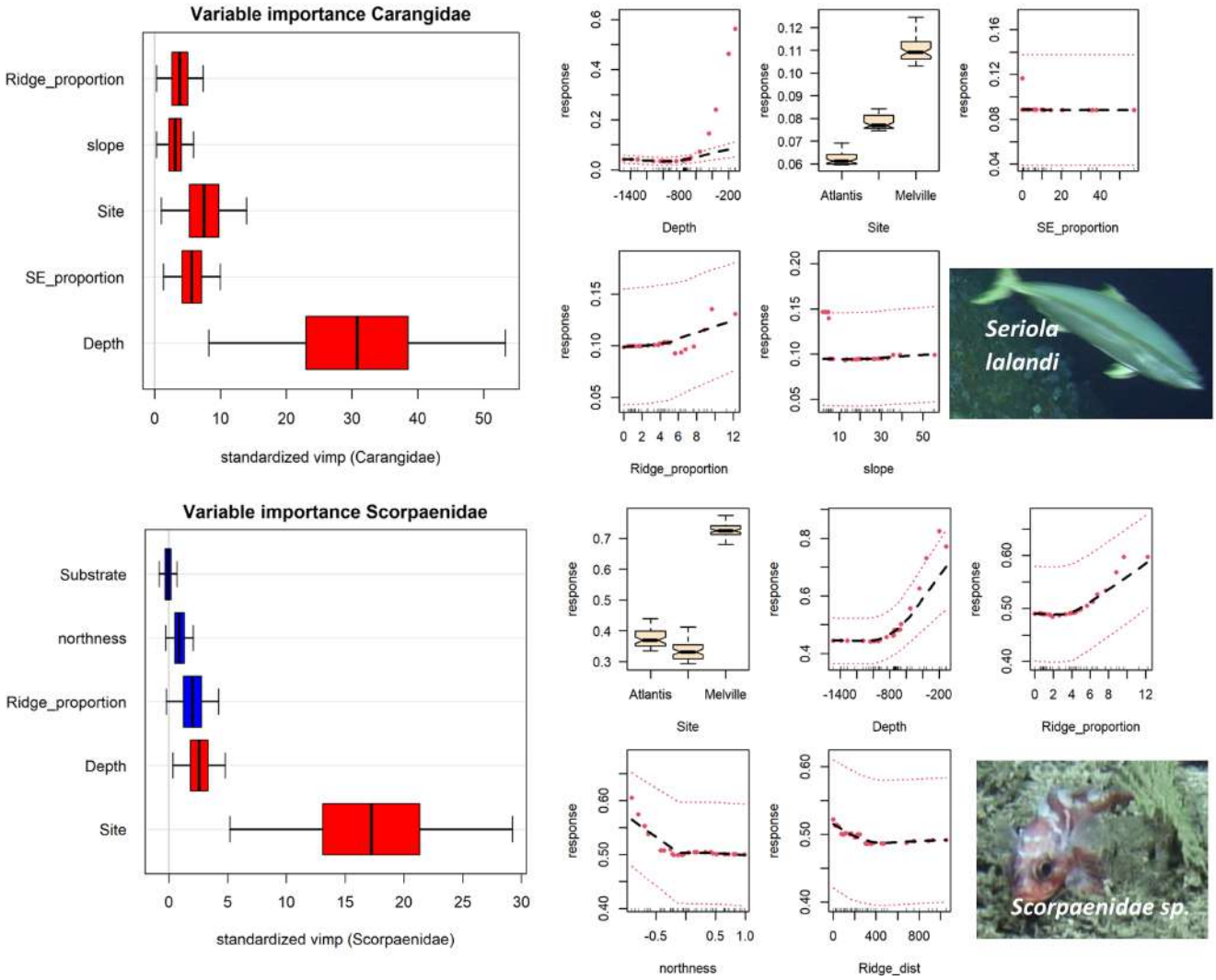


Figure B.4.2: Variable importances epipelagic continued

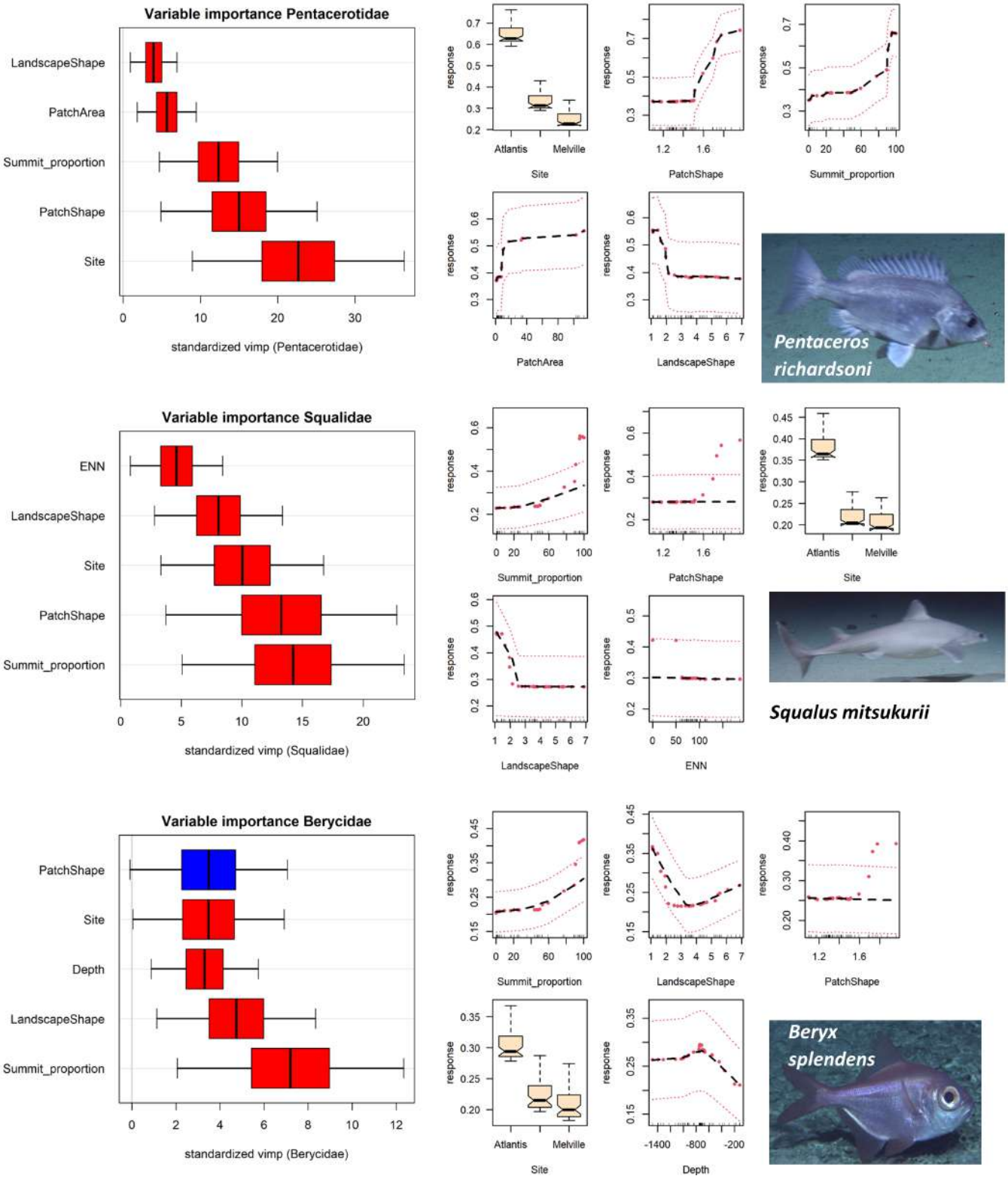


Figure B.4.3: Variable importances mesopelagic. Blue indicates non significant (P<0.05) effect

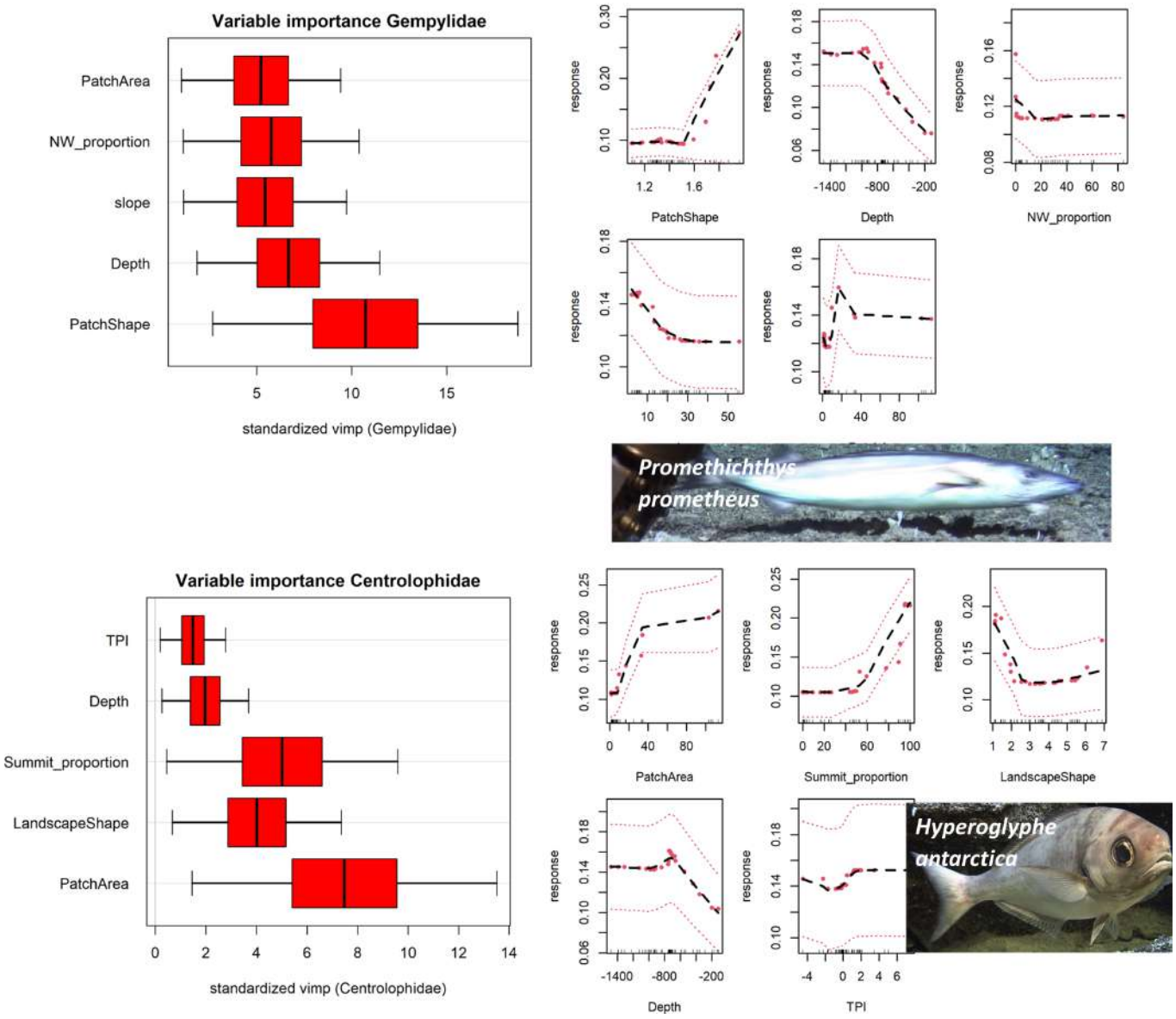


Figure B.4.4: Variable importances mesopelagic continued

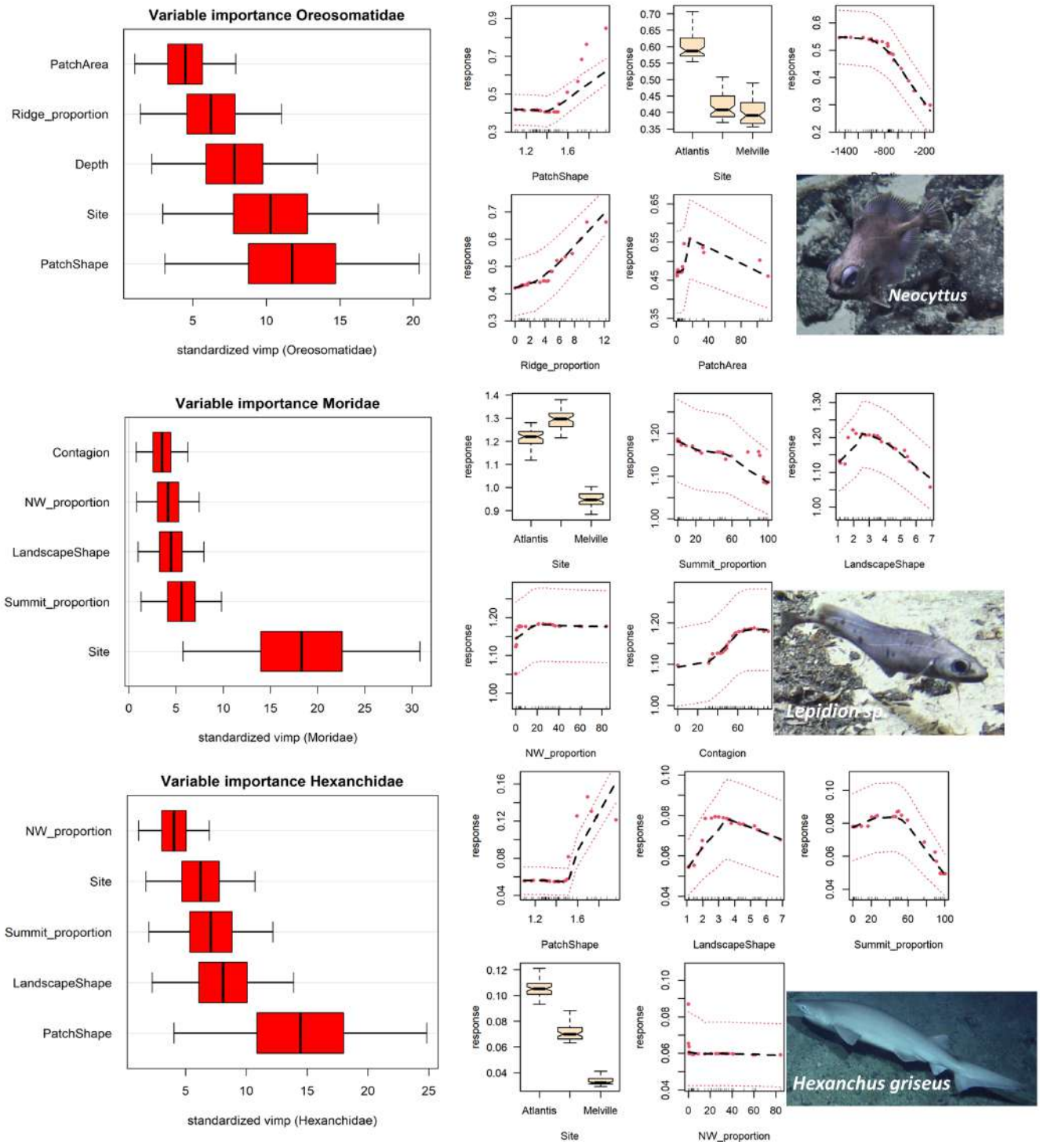


Figure B.4.5: Variable importances bathypelagic. Blue indicates non significant (P<0.05) effect

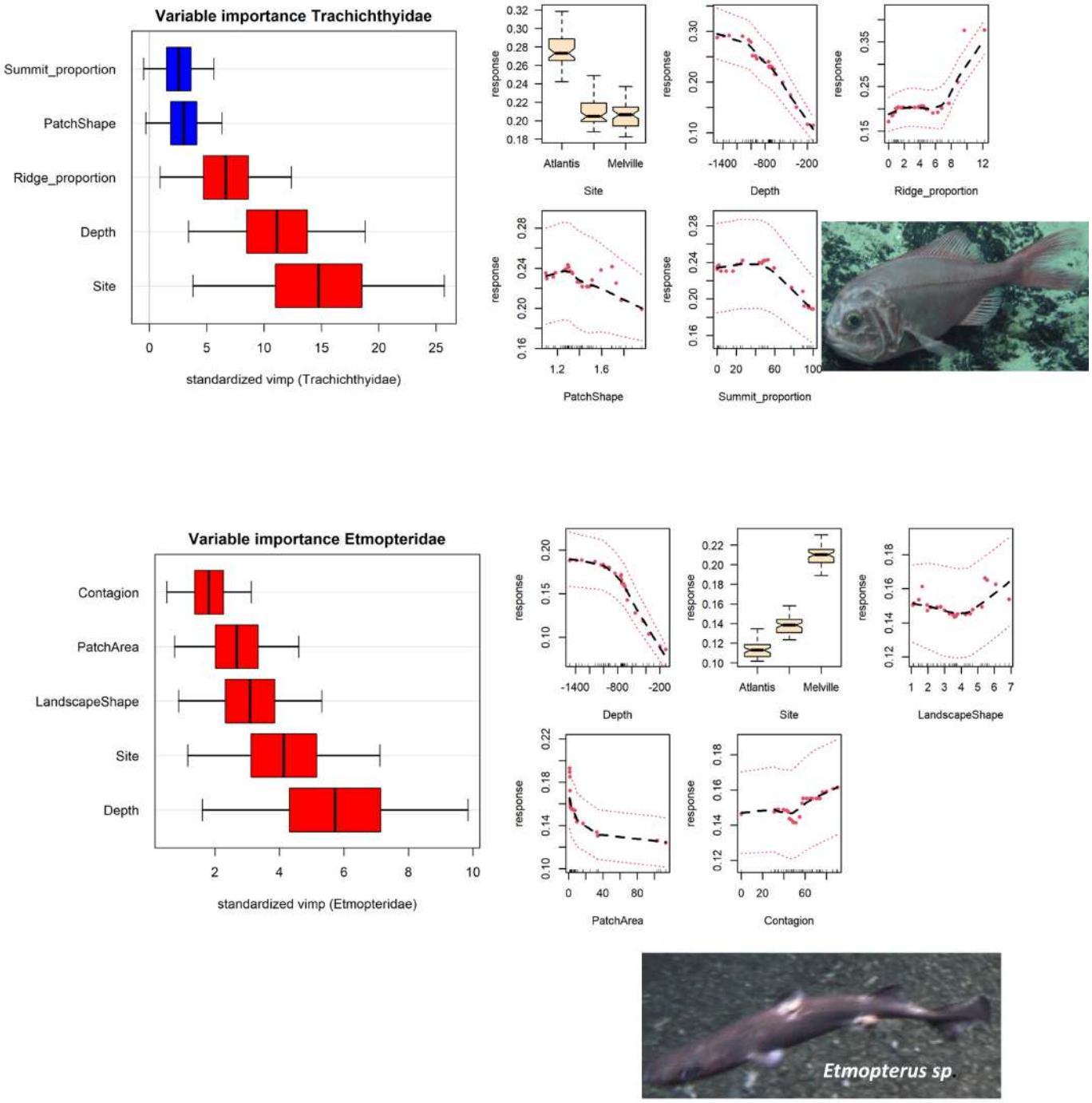


Figure B.4.6: Variable importances bathypelagic continued

C Appendices to Chapter 4

C.1 Backscatter

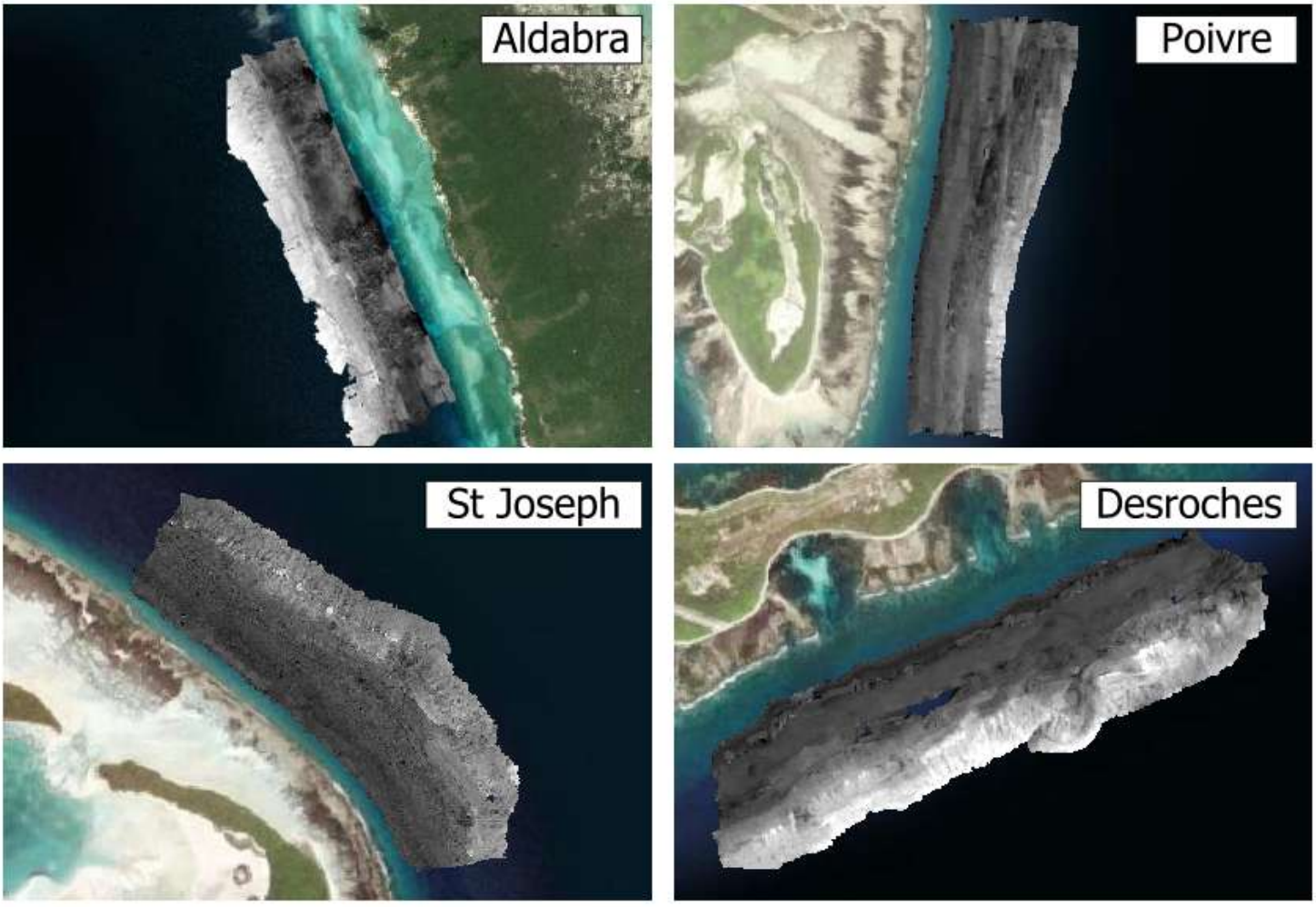


Figure C.1.1: Backscatter data collected at the four survey sites

C.2 Biological data preparation

Table C.2.1: *Observations per site per assemblage cluster. Observations correspond to the number of images containing that assemblage type and data points used for subsequent analysis*

Location	Total observations	Absence of benthic organisms	Assemblage 1	Assemblage 2	Assemblage 3	Assemblage 4
St. Joseph	446	218	56	55	73	48
Desroches	367	72	102	86	85	25
Poivre	415	58	101	62	159	35
Aldabra	540	272	56	82	101	23

Table C.2.2: *PERMANOVA results testing for significant differences between assemblage clusters. Outputs indicate significant differences between assemblage clusters at all sites*

	Df	Sum of Squares	R2	Pr(>F)
St. Joseph				
Cluster	1	12.253	0.149	<0.001***
Residual	204	70.192	0.851	
Total	205	82.446	1.000	
Desroches				
Cluster	1	13.437	0.1251	<0.001***
Residual	294	93.974	0.875	
Total	295	107.412	1.000	
Poivre				
Cluster	1	23.188	0.216	<0.001***
Residual	355	83.836	0.783	
Total	356	107.24	1.000	
Aldabra				
Cluster	1	10.086	0.098	<0.001***
Residual	255	92.583	0.902	
Total	256	102.668	1.000	

C.3 Model performance outputs

Table C.3.1: *Model performance measured in AUC, MAE, Moran's I and visual accuracy per site. Moran's I numbers in bold represent significant spatial autocorrelation ($p<0.05$)*

Aldabra	**Random Forests**						**Boosted Regression Trees**					
	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual
Assemblage 1	0.925	0.029	0.157	0.039	0.058	Partly	0.920	0.040	0.167	0.037	-0.052	Partly
Assemblage 2	0.893	0.024	0.142	0.027	0.051	Yes	0.880	0.037	0.163	0.028	-0.075	Yes
Assemblage 3	1.000	0.000	0.023	0.012	0.011	Yes	0.990	0.004	0.025	0.008	0.036	Yes
Assemblage 4	0.894	0.035	0.052	0.013	**0.389**	Yes	0.930	0.035	0.062	0.011	**0.435**	Partly
Poivre	**Random Forests**						**Boosted Regression Trees**					
	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual
Assemblage 1	0.969	0.022	0.096	0.025	-0.032	Yes	0.975	0.017	0.102	0.025	-0.001	No
Assemblage 2	0.833	0.091	0.229	0.034	0.094	Partly	0.824	0.112	0.248	0.037	0.117	Partly
Assemblage 3	0.983	0.025	0.063	0.026	-0.013	Yes	0.980	0.031	0.070	0.032	-0.004	Yes
Assemblage 4	0.997	0.007	0.043	0.014	**0.399**	No	0.996	0.007	0.046	0.018	**0.265**	No
St. Joseph	**Random Forests**						**Boosted Regression Trees**					
	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual
Assemblage 1	0.882	0.046	0.162	0.033	0.024	Yes	0.912	0.042	0.184	0.030	0.041	Yes
Assemblage 2	0.908	0.026	0.149	0.040	-0.026	Yes	0.907	0.032	0.160	0.039	-0.020	No
Assemblage 3	0.989	0.006	0.039	0.019	0.014	Yes	0.982	0.004	0.057	0.029	0.091	Yes
Assemblage 4	0.864	0.077	0.154	0.043	**0.138**	Yes	0.856	0.047	0.166	0.043	**0.143**	Partly
Desroches	**Random Forests**						**Boosted Regression Trees**					
	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual	AUC (mean)	AUC (sd)	MAE (mean)	MAE (sd)	Moran's I	Visual
Assemblage 1	0.989	0.019	0.044	0.029	-0.059	Yes	0.990	0.008	0.055	0.028	-0.050	No
Assemblage 2	0.963	0.022	0.111	0.028	0.049	Yes	0.965	0.011	0.122	0.020	-0.076	Partly
Assemblage 3	0.974	0.030	0.039	0.015	0.046	Yes	0.986	0.001	0.045	0.017	0.034	Yes
Assemblage 4	0.970	0.026	0.072	0.044	**0.188**	Partly	0.971	0.028	0.080	0.042	**0.124**	Yes

C.4 Partial dependence plots

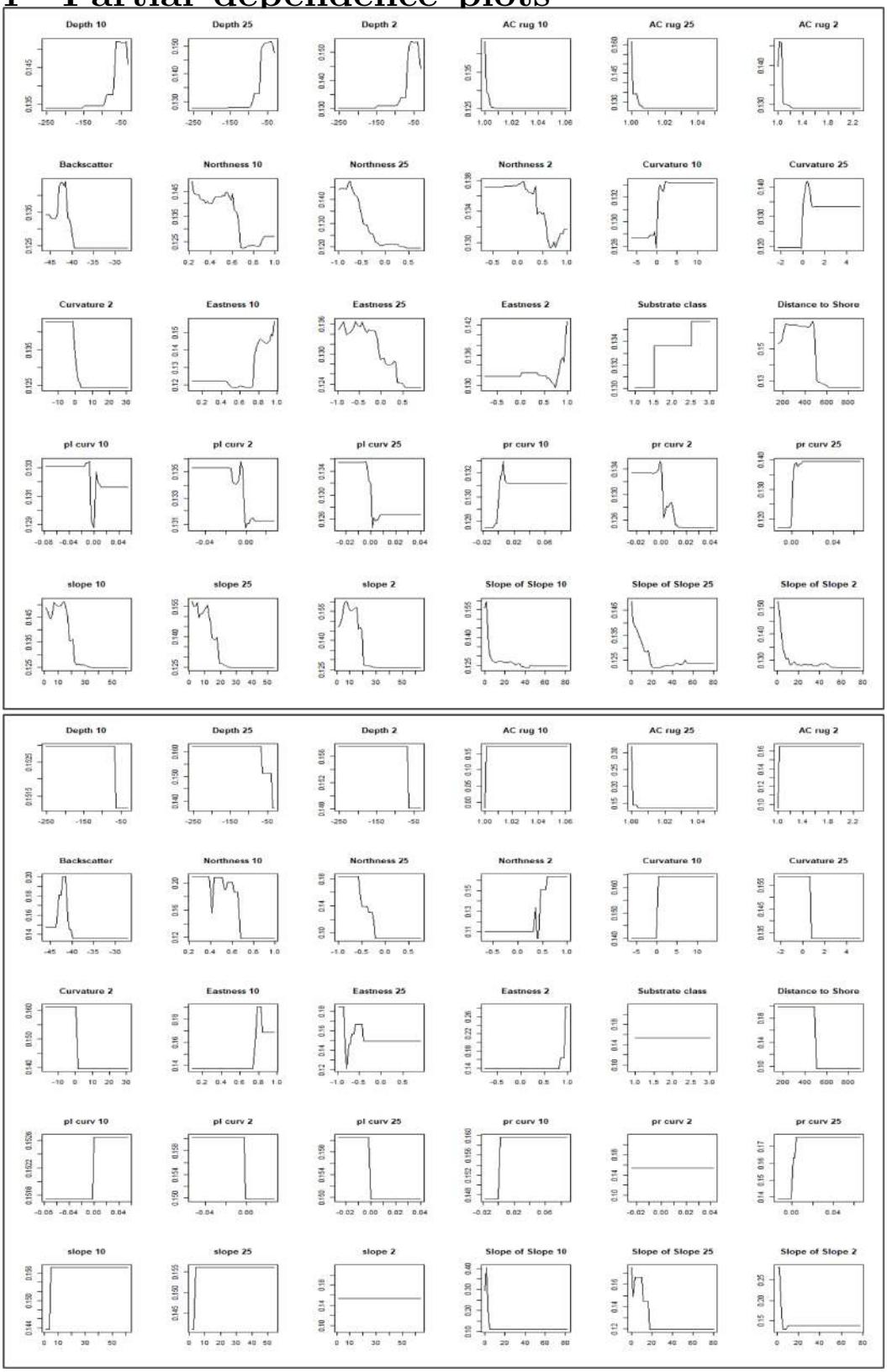


Figure C.4.1: Partial dependency plots for assemblage 1 at St Joseph for RF (top) and BRT (bottom)

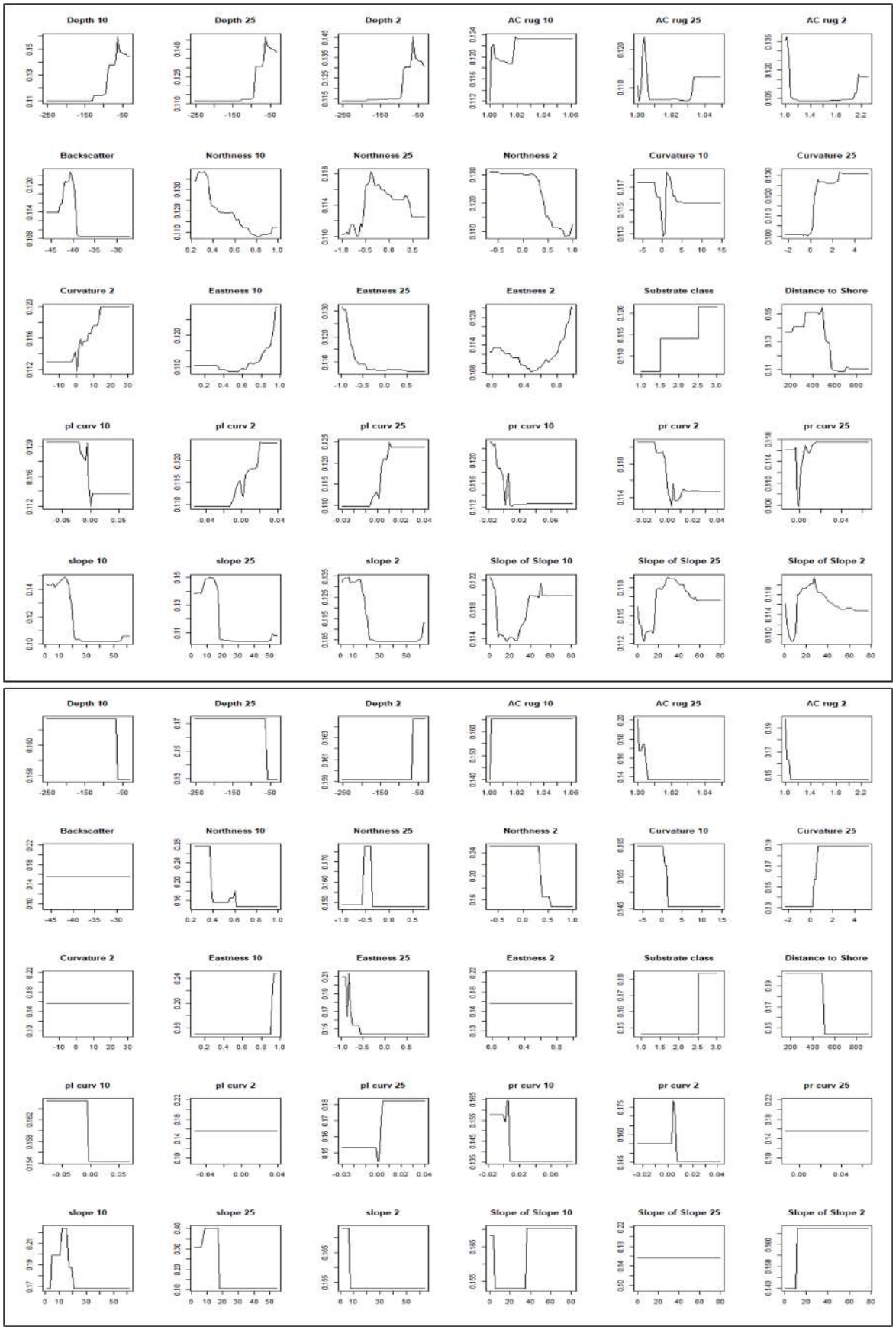


Figure C.4.2: Partial dependency plots for assemblage 2 at St Joseph for RF (top) and BRT (bottom)

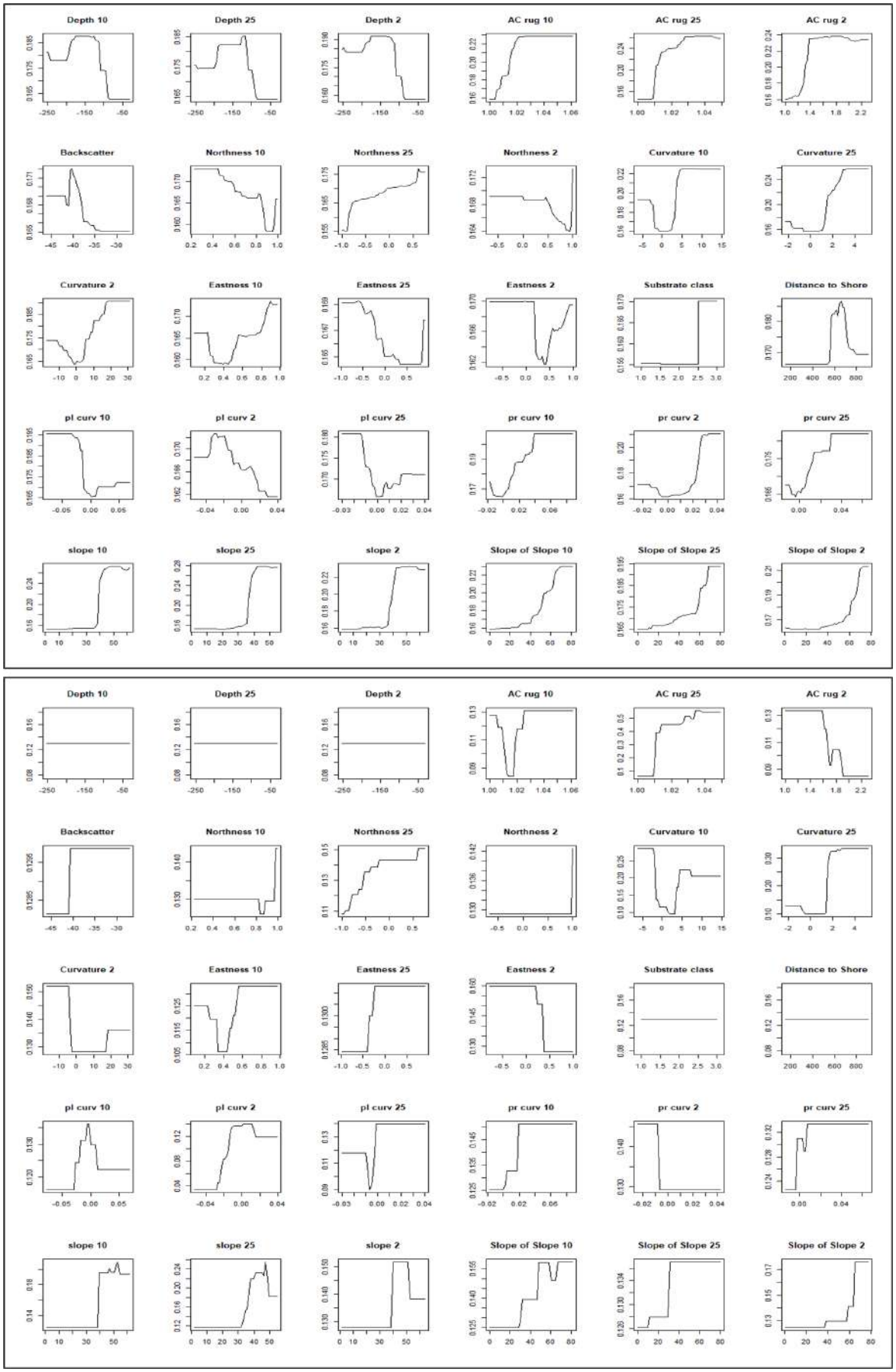


Figure C.4.3: Partial dependency plots for assemblage 3 at St Joseph for RF (top) and BRT (bottom)

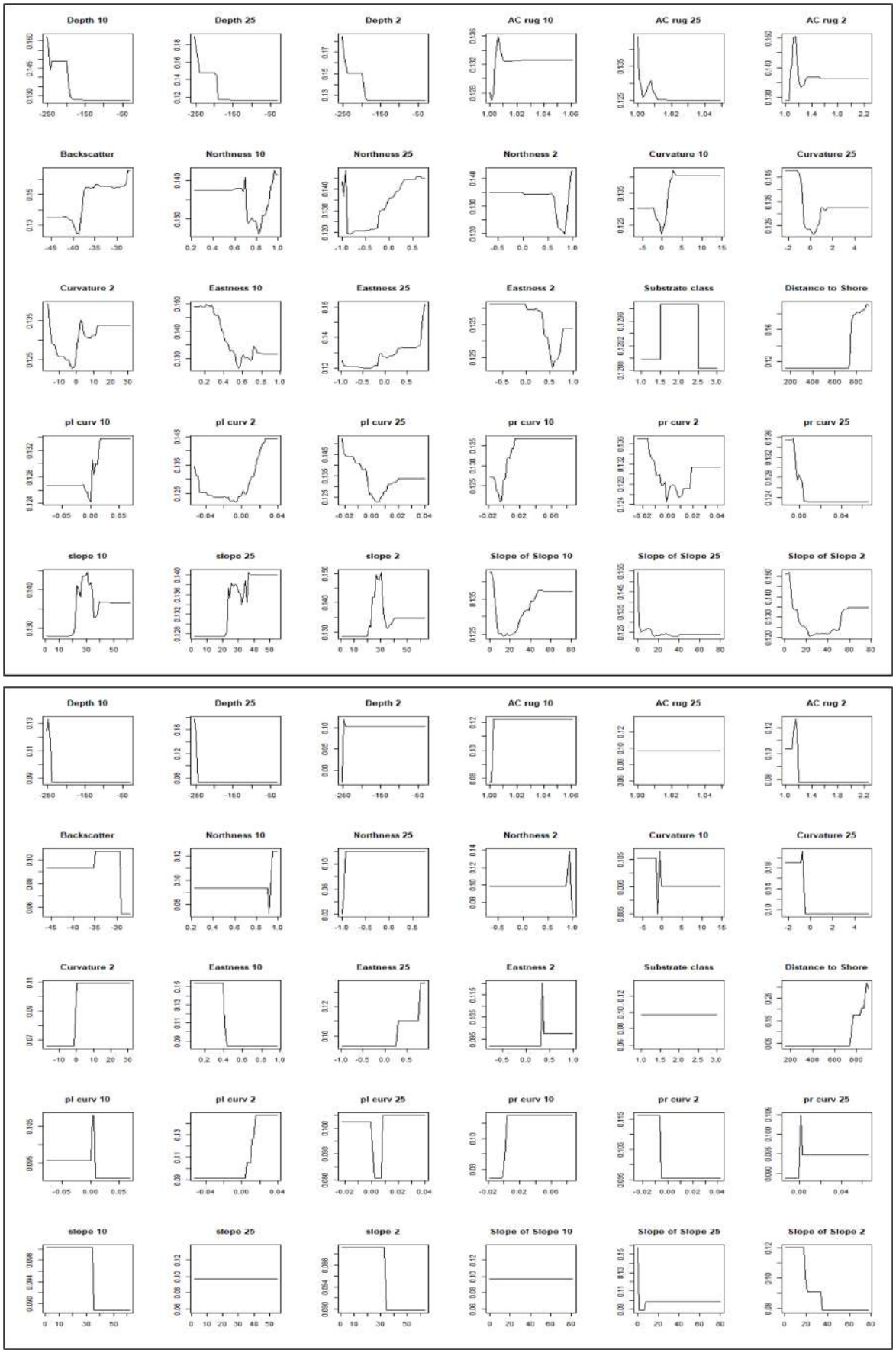


Figure C.4.4: Partial dependency plots for assemblage 4 at St Joseph for RF (top) and BRT (bottom)

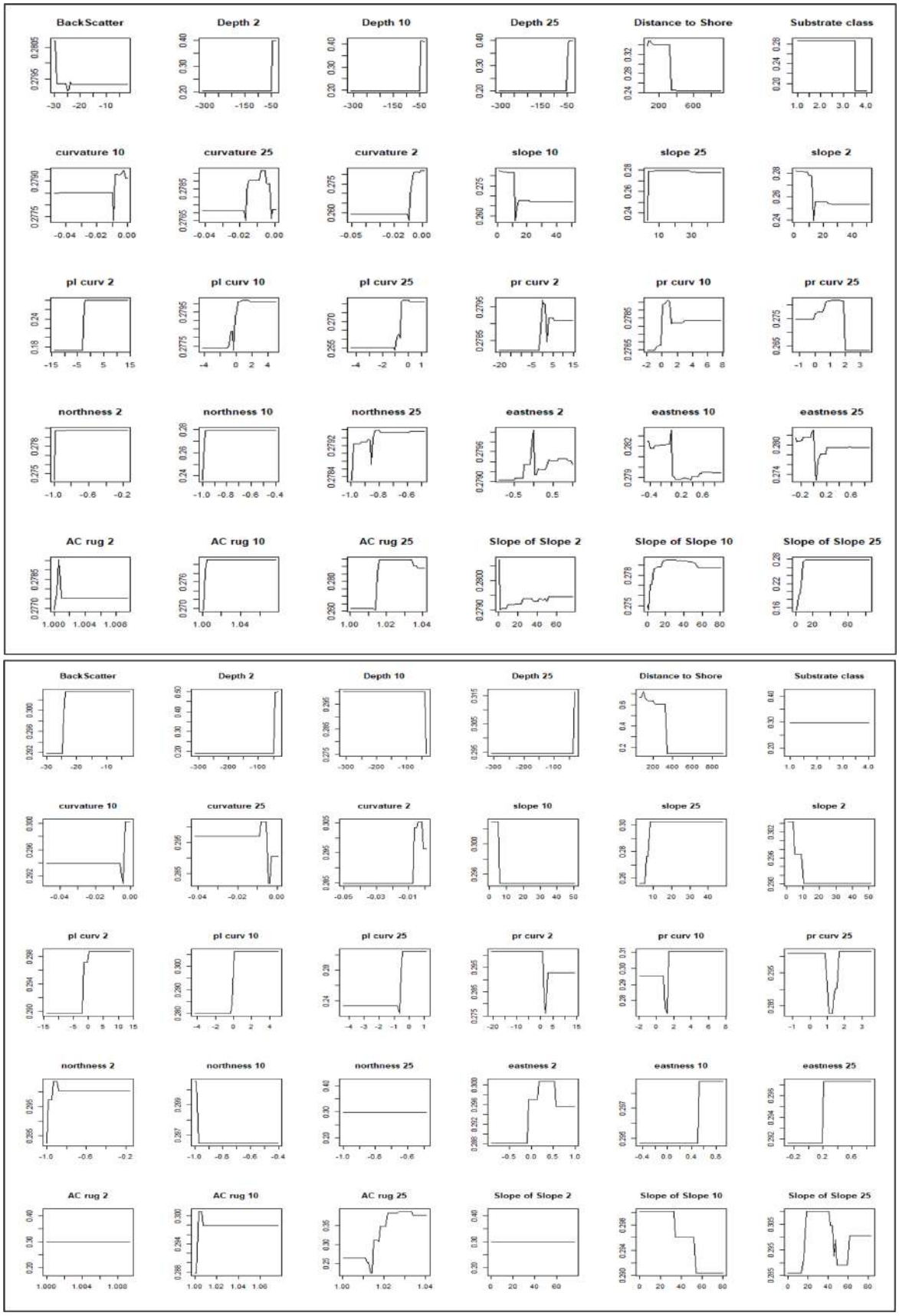


Figure C.4.5: Partial dependency plots for assemblage 1 at Desroches for RF (top) and BRT (bottom)

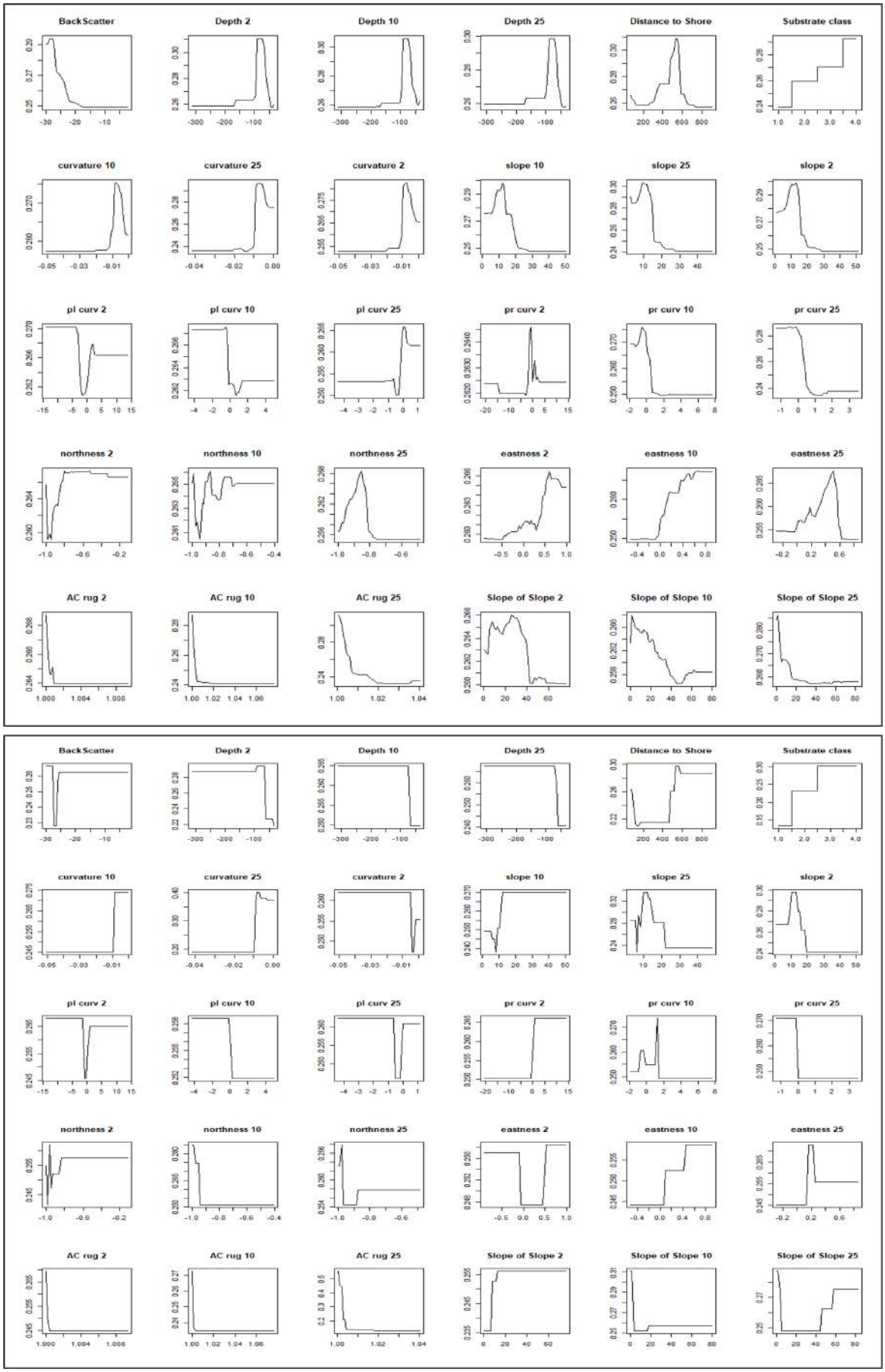


Figure C.4.6: Partial dependency plots for assemblage 2 at Desroches for RF (top) and BRT (bottom)

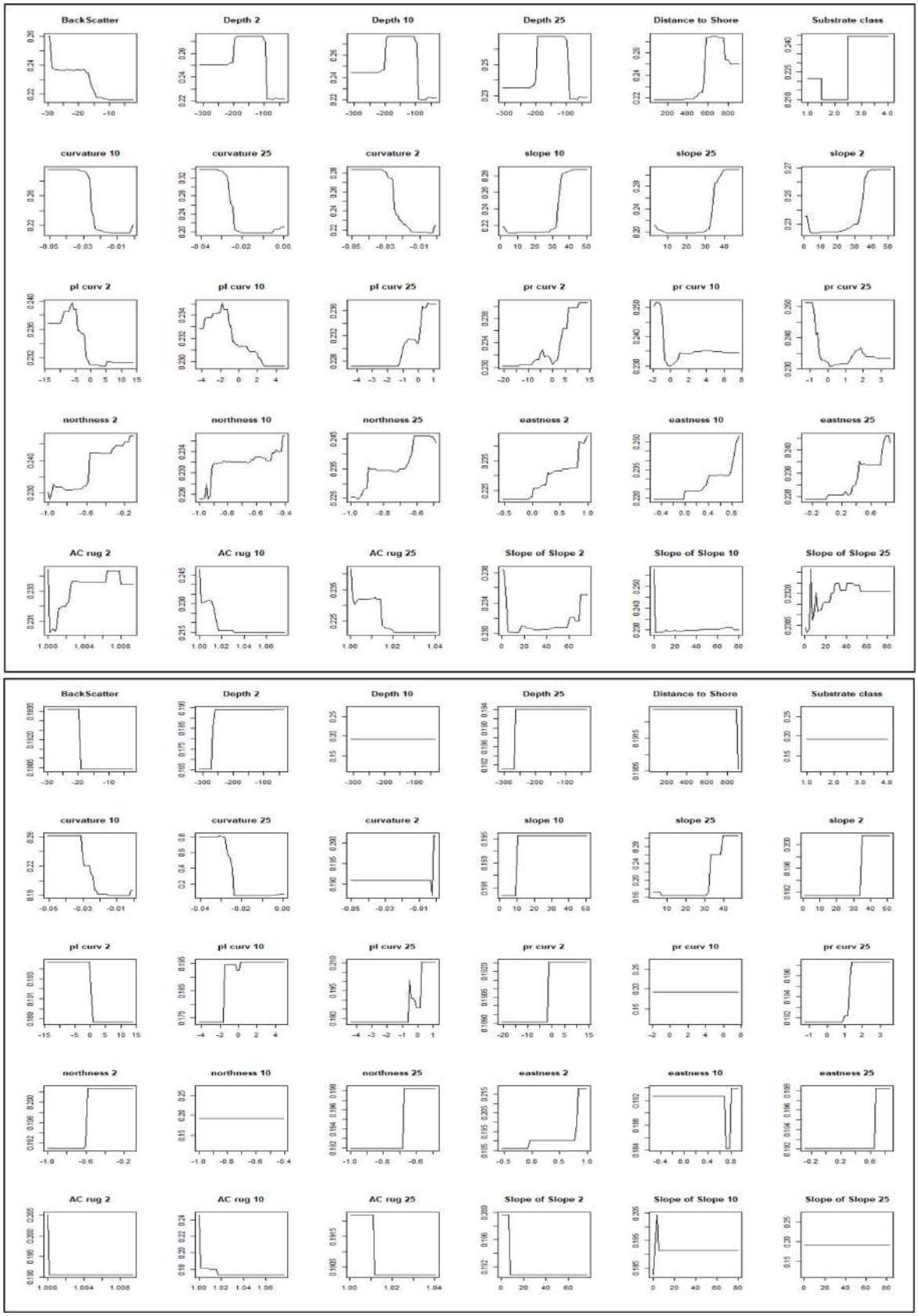


Figure C.4.7: Partial dependency plots for assemblage 3 at Desroches for RF (top) and BRT (bottom)

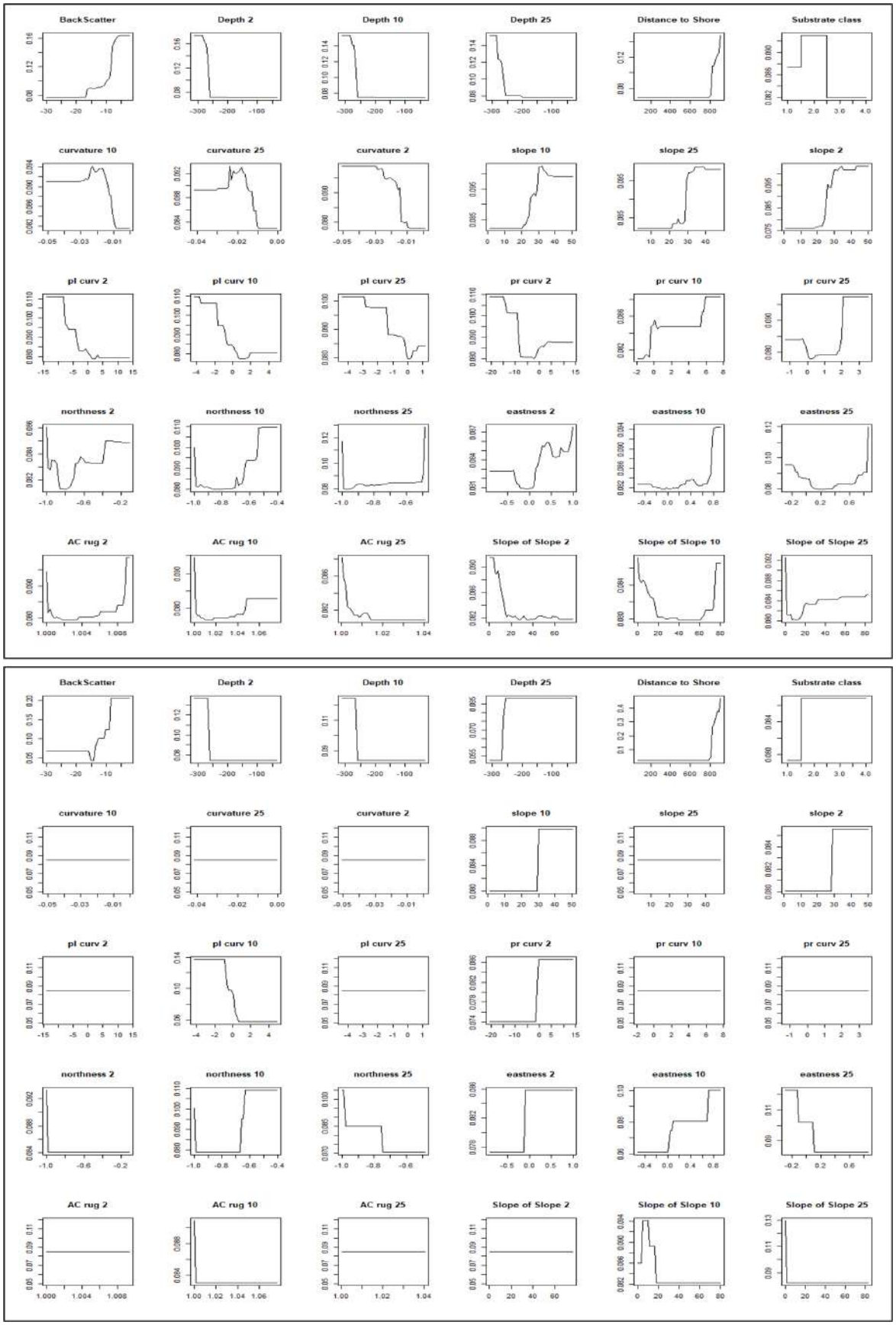


Figure C.4.8: Partial dependency plots for assemblage 4 at Desroches for RF (top) and BRT (bottom)

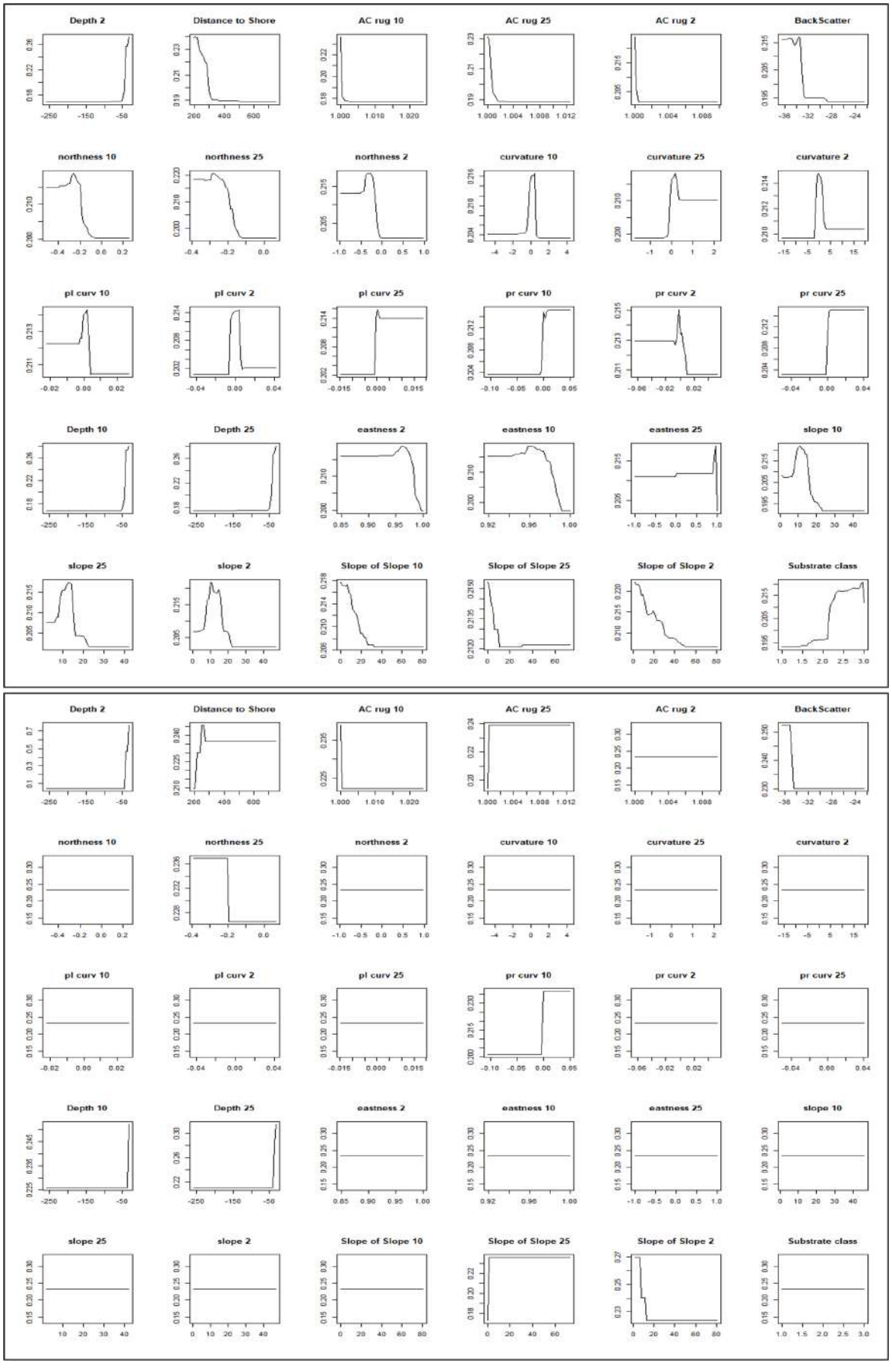


Figure C.4.9: Partial dependency plots for assemblage 1 at Poivre for RF (top) and BRT (bottom)

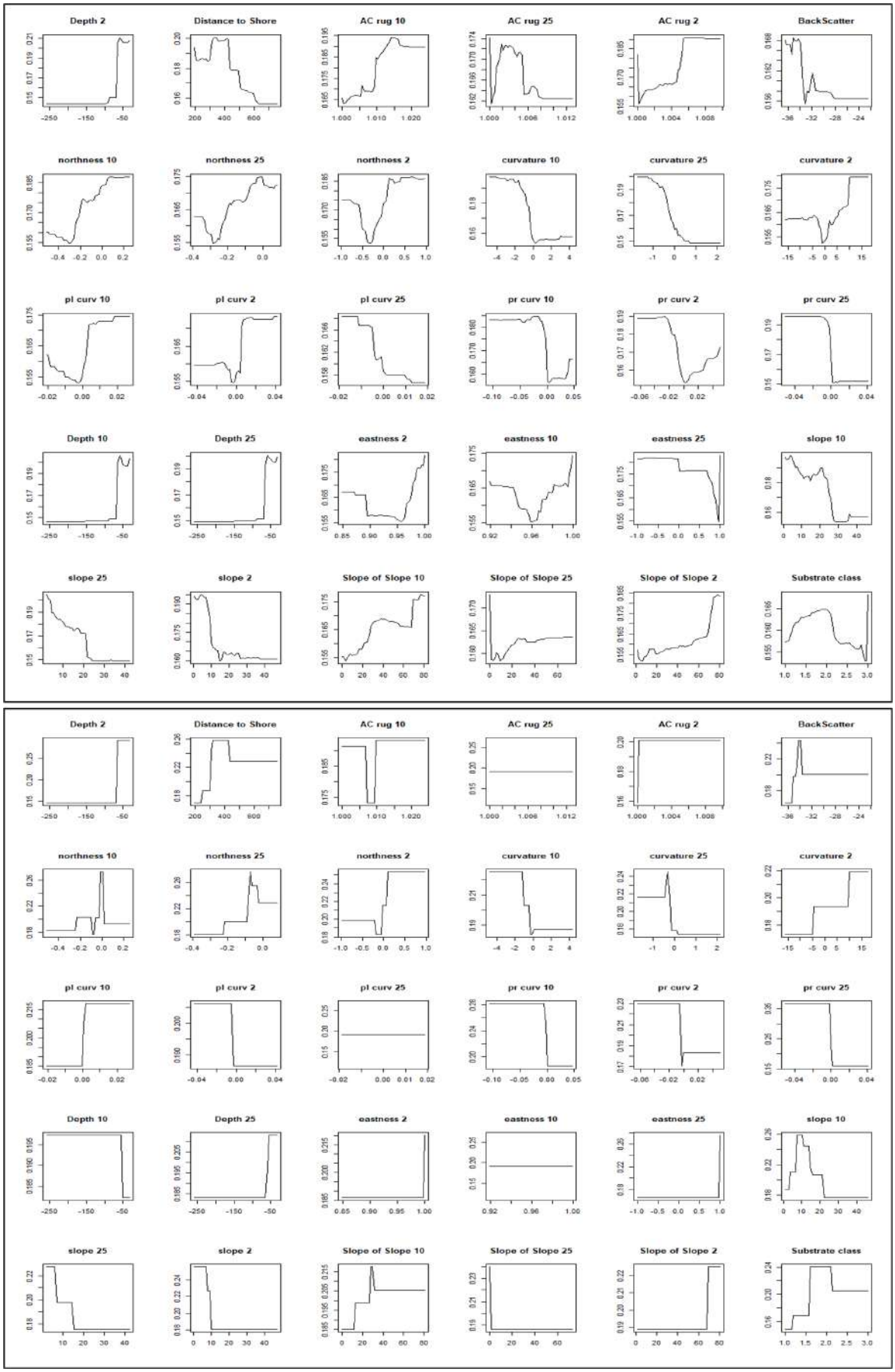


Figure C.4.10: Partial dependency plots for assemblage 2 at Poivre for RF (top) and BRT (bottom)

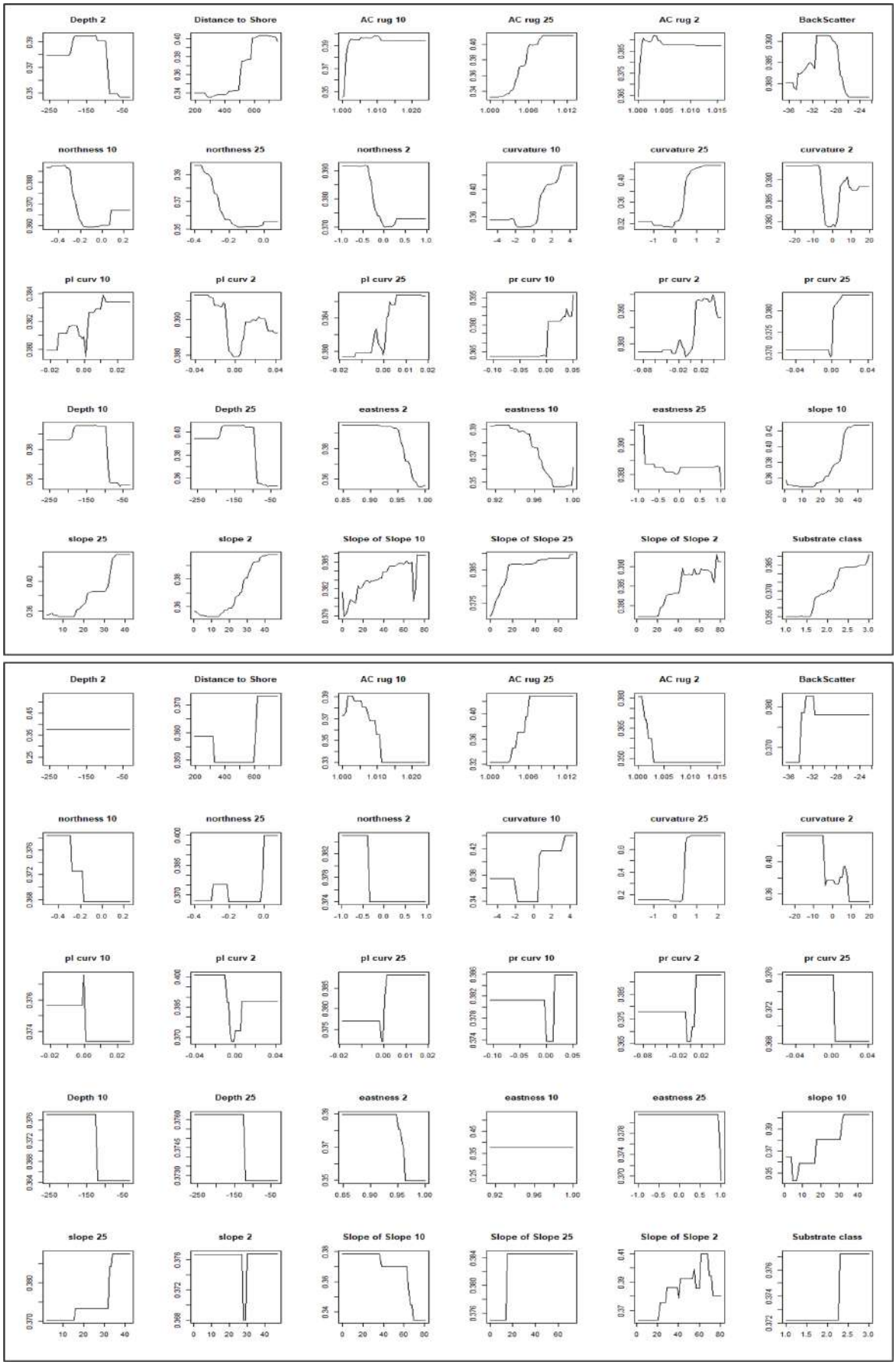


Figure C.4.11: Partial dependency plots for assemblage 3 at Poivre for RF (top) and BRT (bottom)

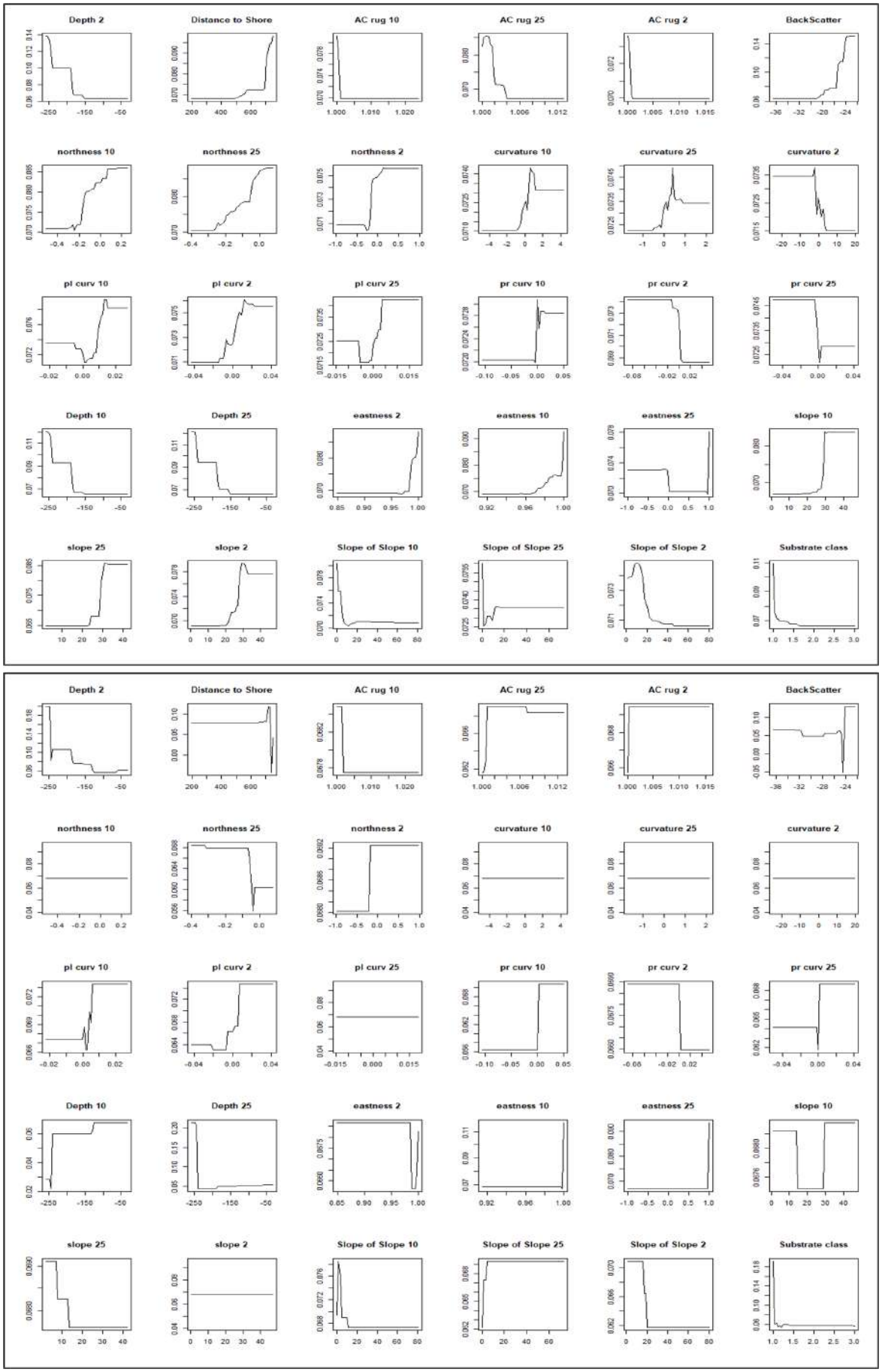


Figure C.4.12: Partial dependency plots for assemblage 4 at Poivre for RF (top) and BRT (bottom)

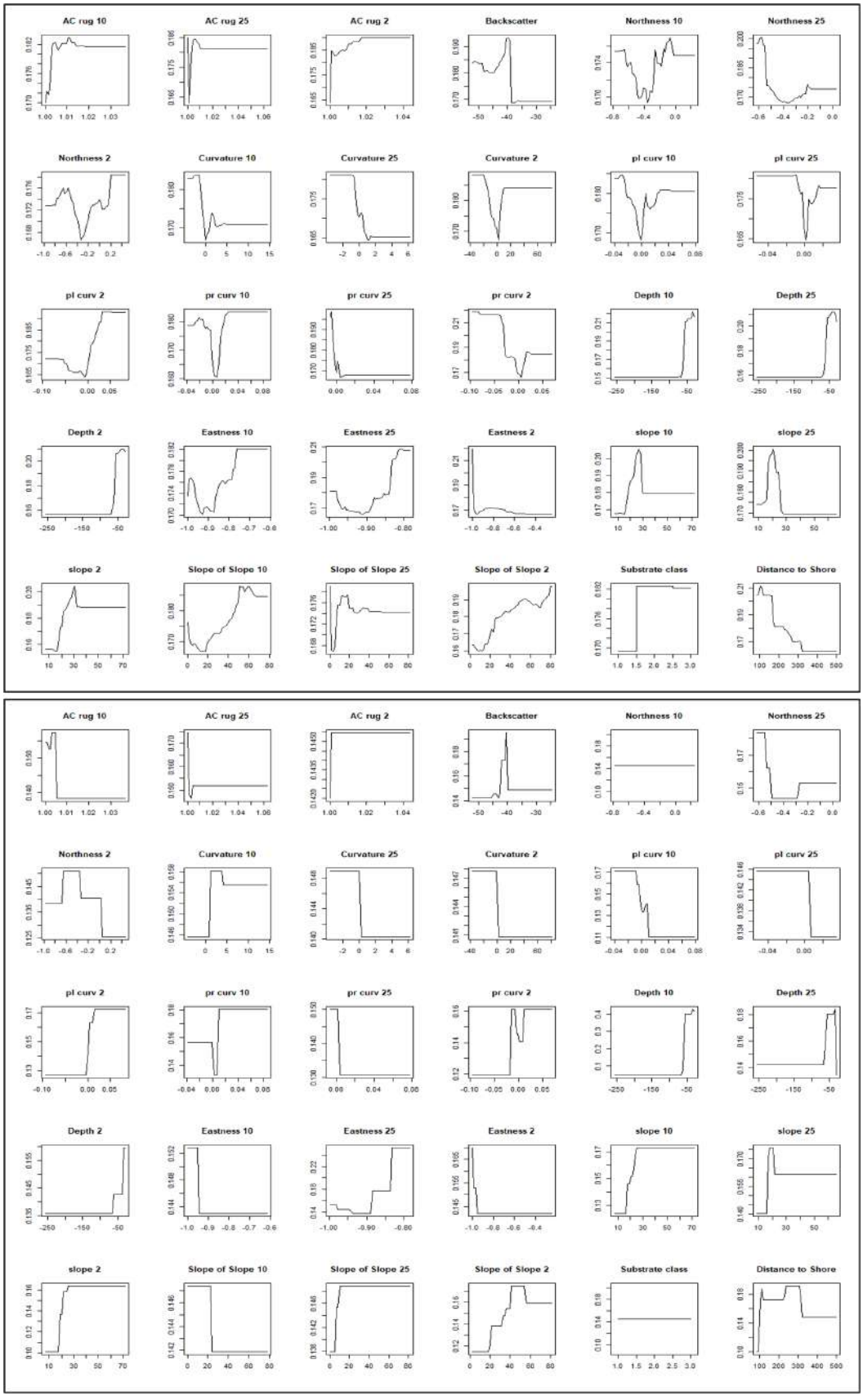


Figure C.4.13: Partial dependency plots for assemblage 1 at Aldabra for RF (top) and BRT (bottom)

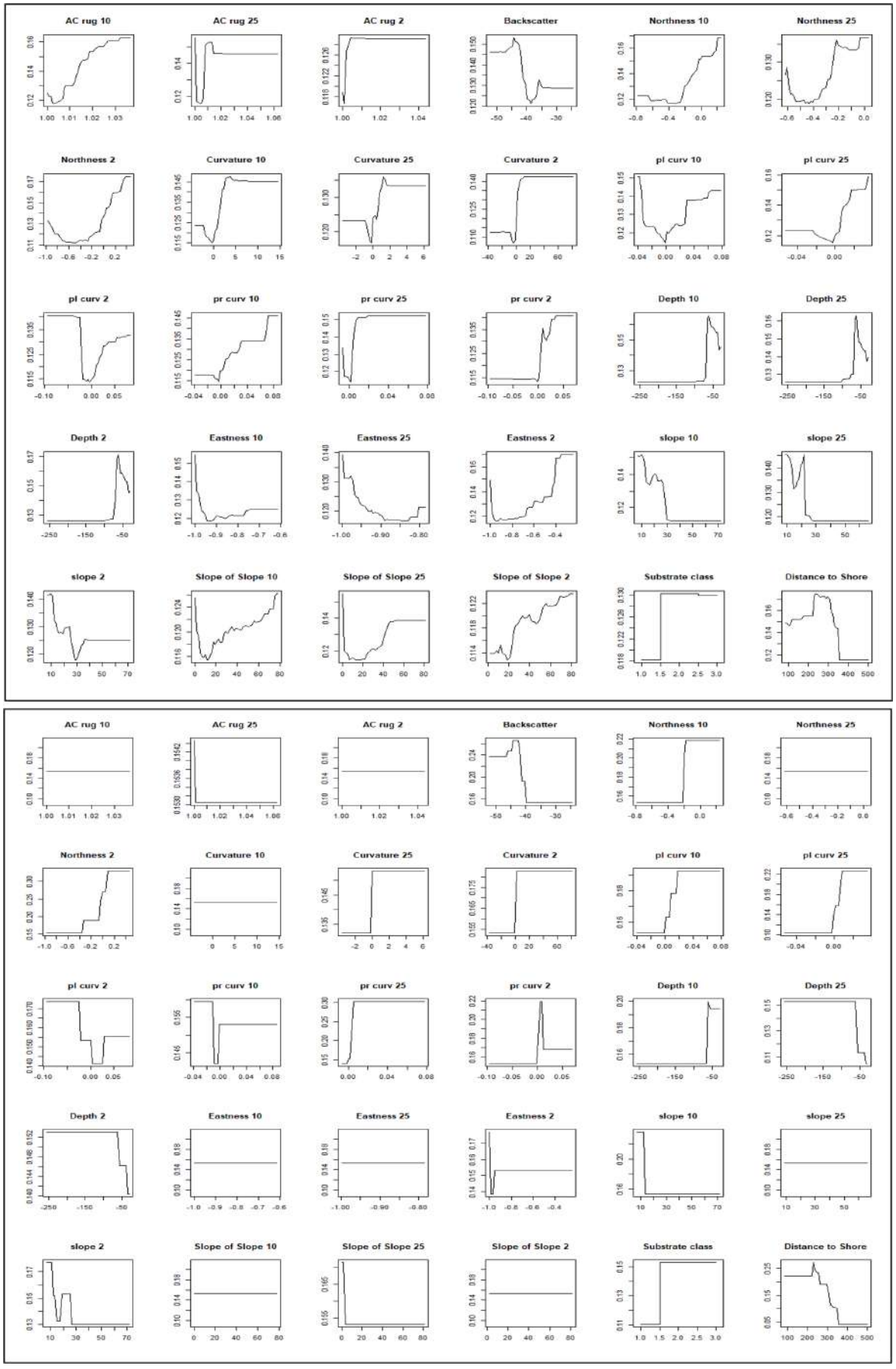


Figure C.4.14: Partial dependency plots for assemblage 2 at Aldabra for RF (top) and BRT (bottom)

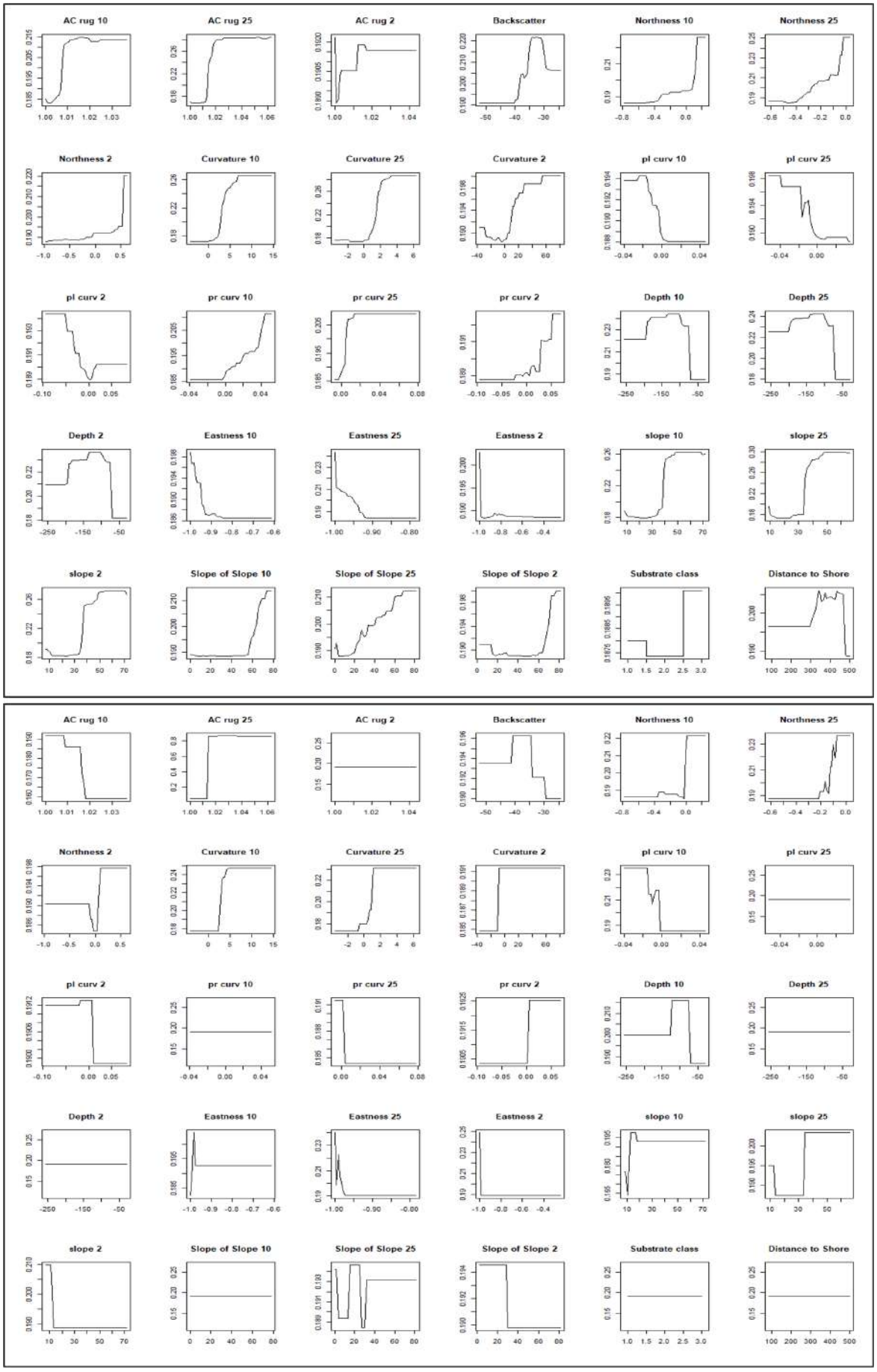


Figure C.4.15: Partial dependency plots for assemblage 3 at Aldabra for RF (top) and BRT (bottom)

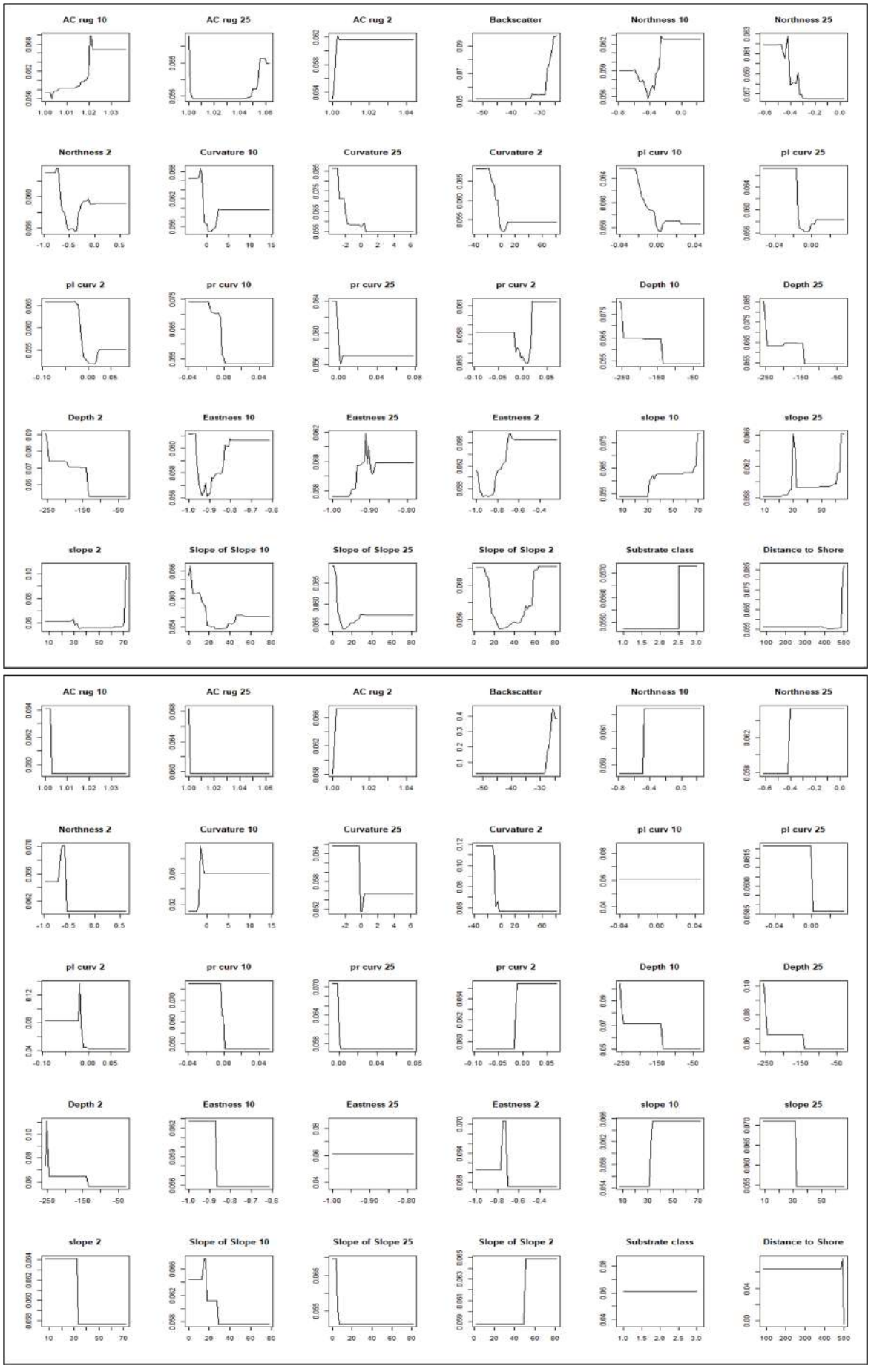


Figure C.4.16: Partial dependency plots for assemblage 4 at Aldabra for RF (top) and BRT (bottom)

C.5 Density plots

Figure C.5.1 to C.5.3 show density plots produced for Aldabra, Poivre and Desroches not displayed in the main text.

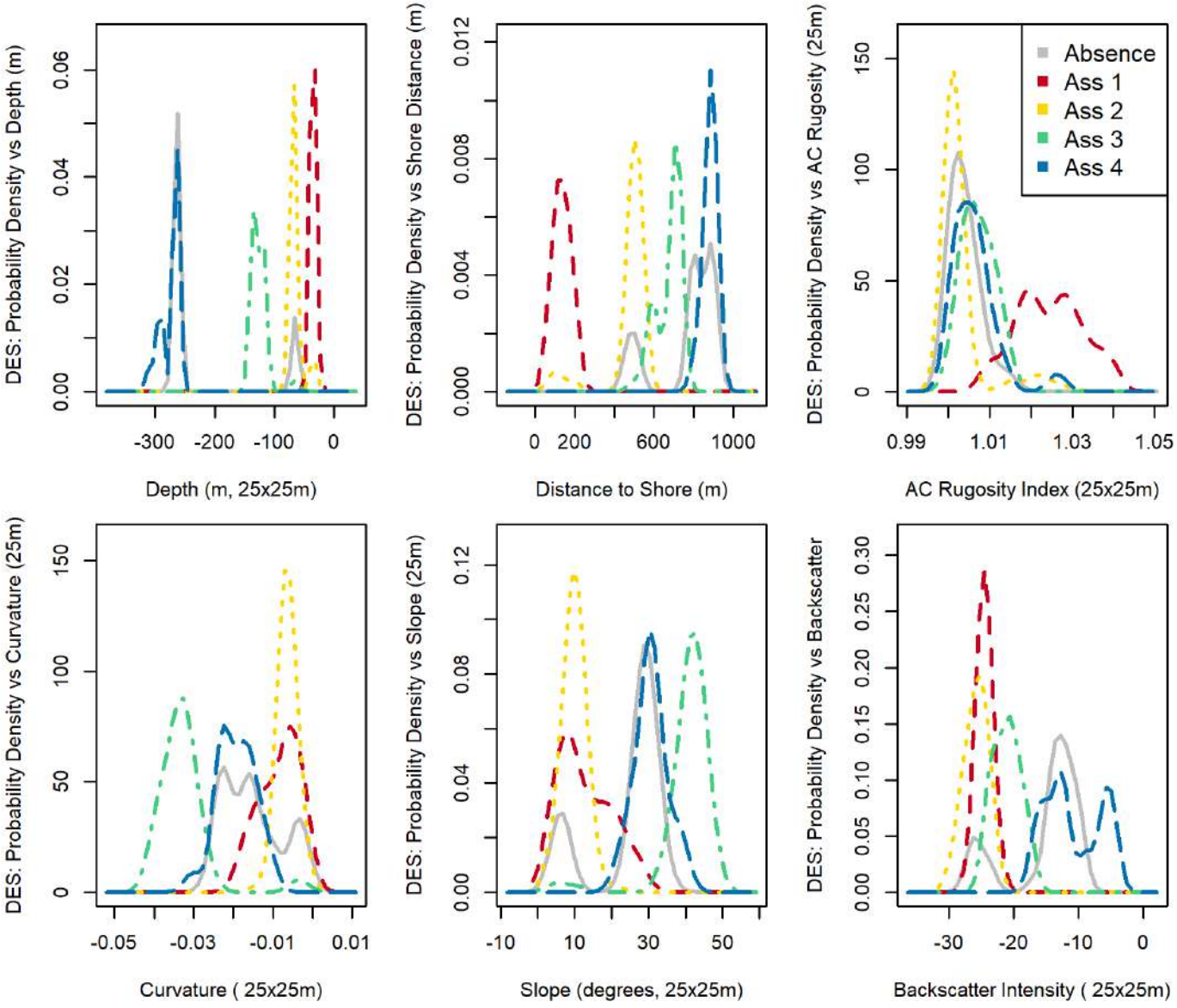


Figure C.5.1: Probability density plots for the overall highest contributing predictors at Desroches

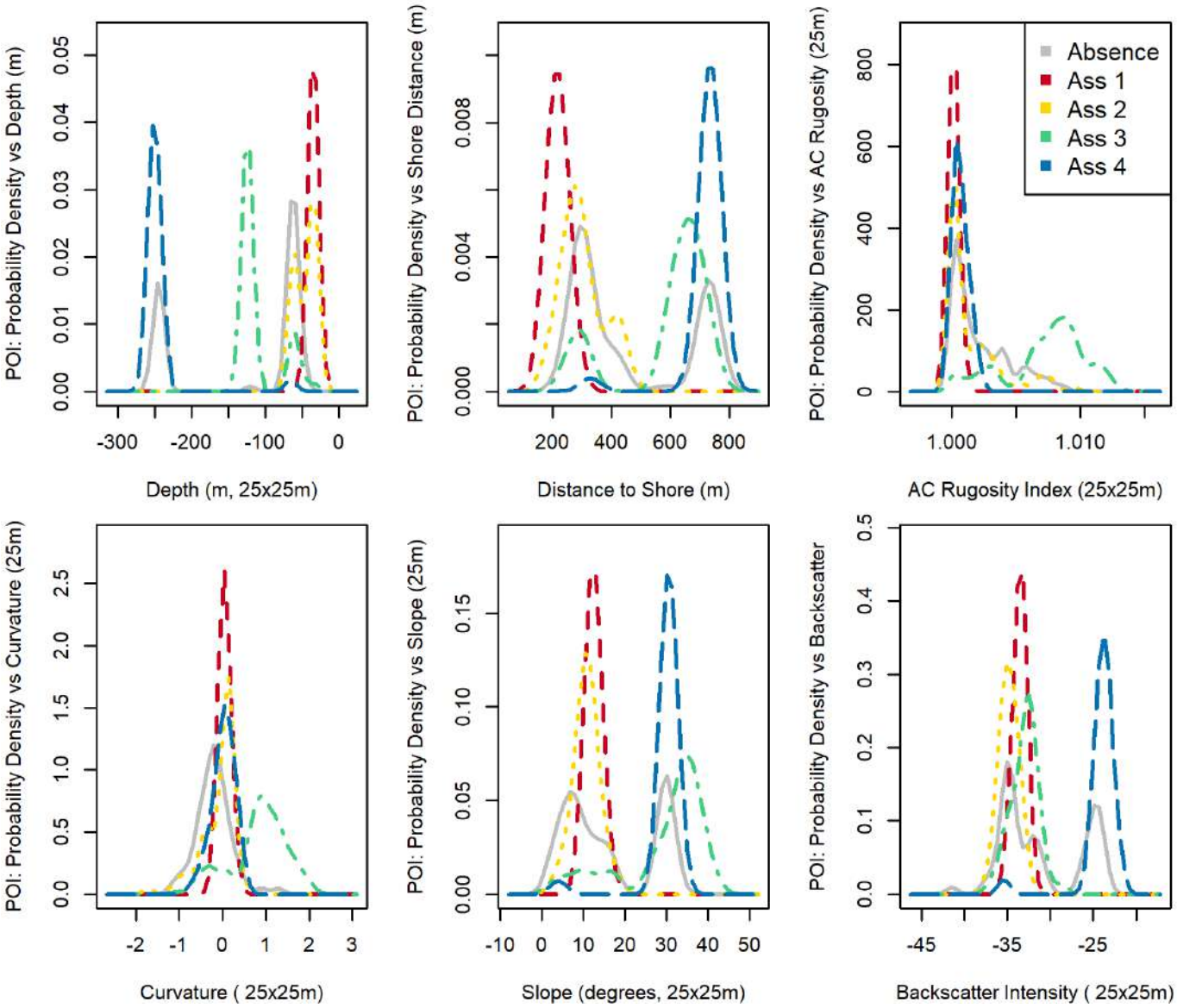


Figure C.5.2: Probability density plots for the overall highest contributing predictors at Poivre

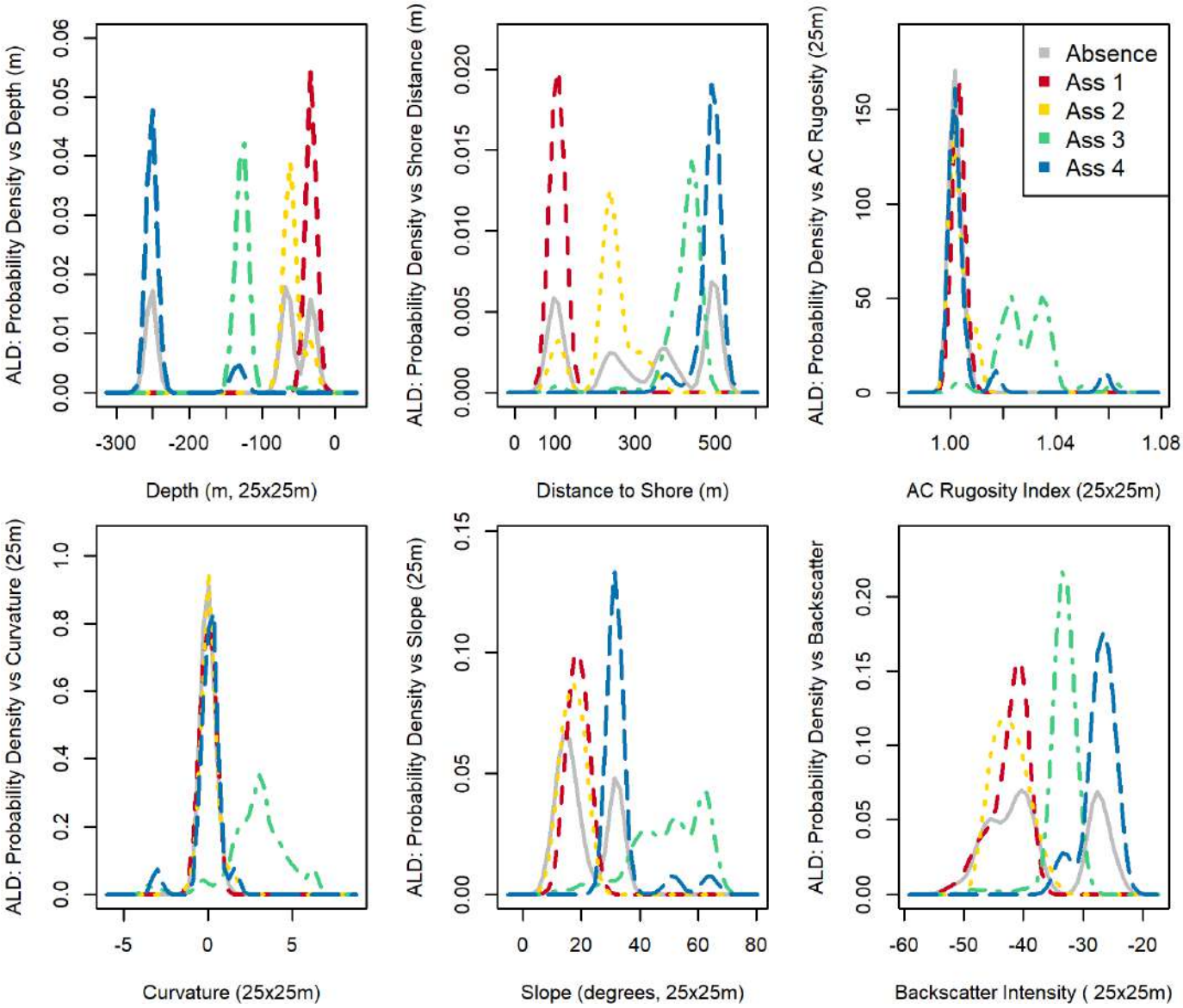


Figure C.5.3: Probability density plots for the overall highest contributing predictors at Aldabra

C.6 Spatial predictions

Figure C.6.1 to C.6.3 show predictive maps produced for Aldabra, Poivre and Desroches not displayed in the main text.

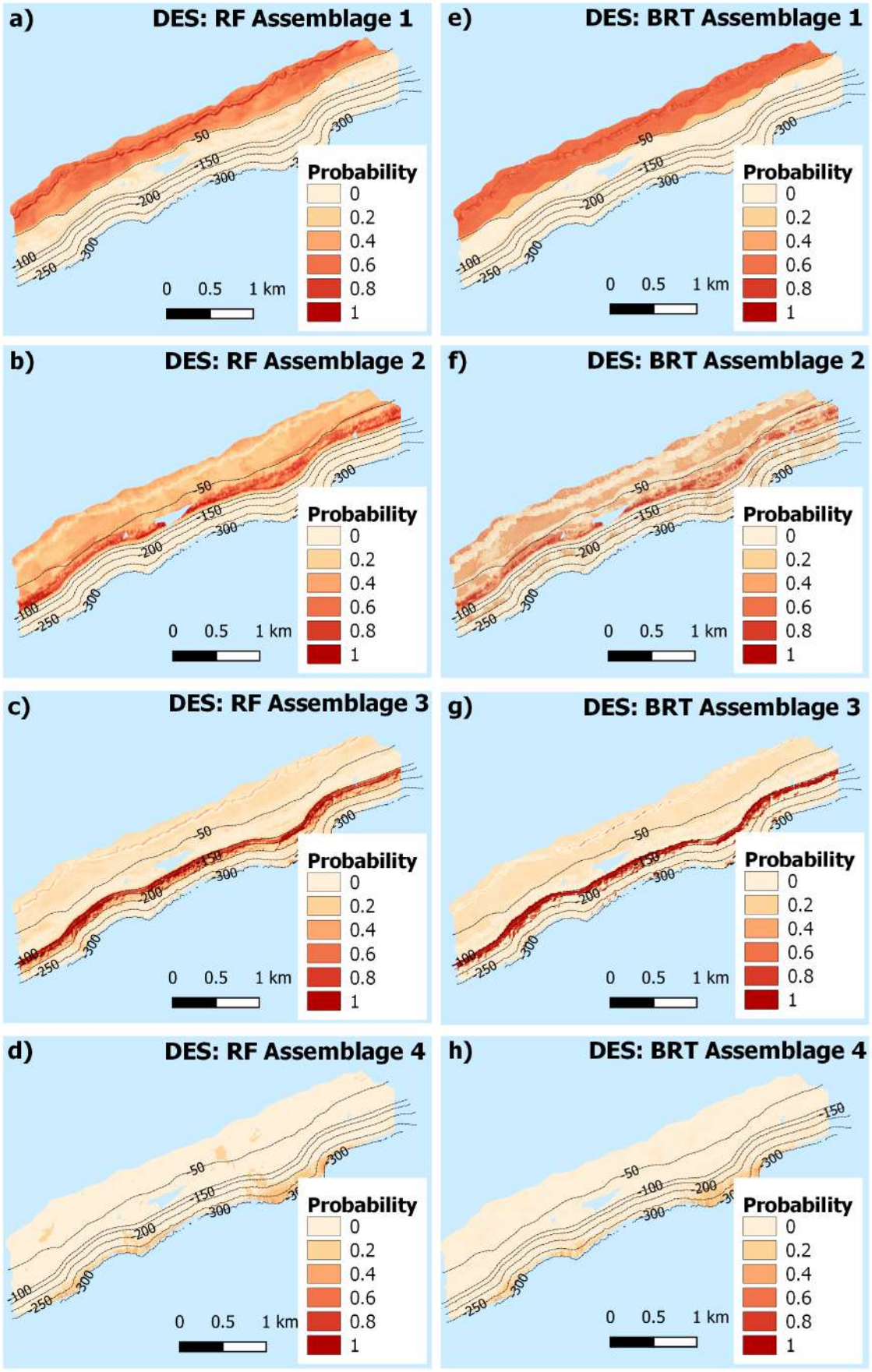


Figure C.6.1: Spatial predictions for deeper reef assemblages at Desroches using Random Forests (a-d) and Boosted Regression Trees (e-h)

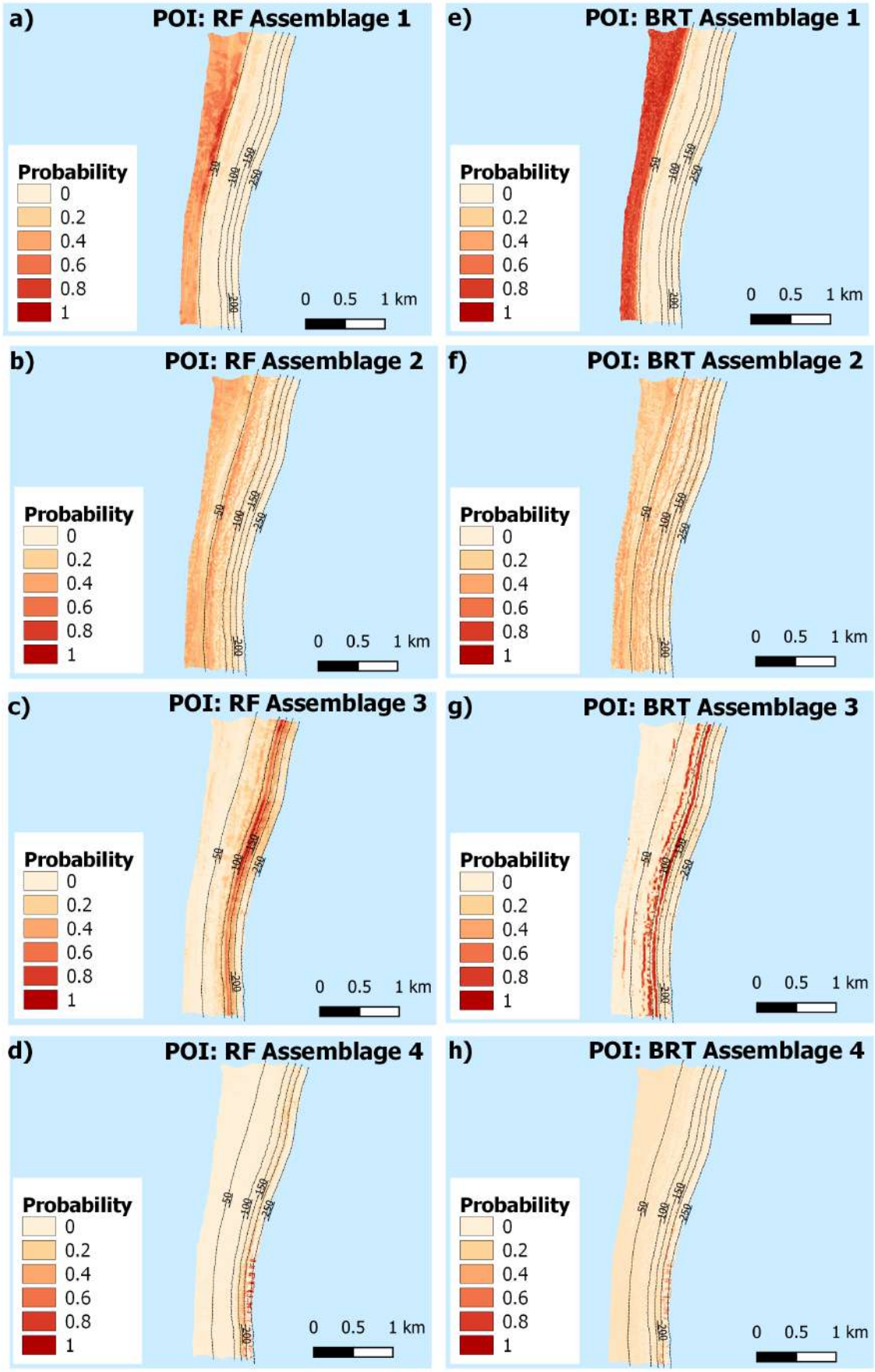


Figure C.6.2: Spatial predictions for deeper reef assemblages at Poivre using Random Forests (a-d) and Boosted Regression Trees (e-h)

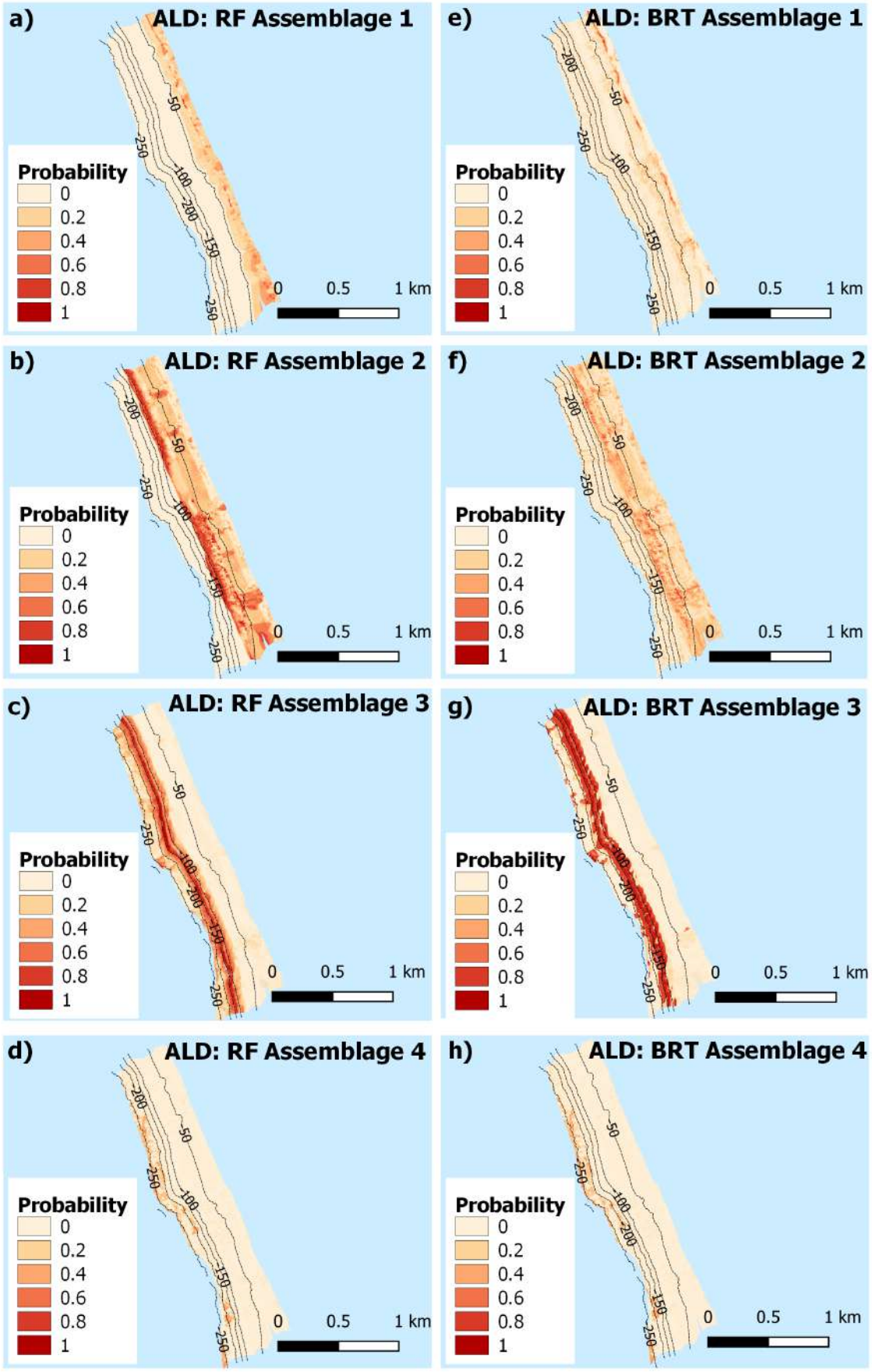


Figure C.6.3: Spatial predictions for deeper reef assemblages at Aldabra using Random Forests (a-d) and Boosted Regression Trees (e-h)

D Appendices to Chapter 5

D.1 Photogrammetry parameters

Table D.1.1: *SfM photogrammetry reconstruction parameters used in Agisoft Metashape*

Step	Construction parameters
1. Alignment and construction point could	Medium accuracy, generic preselection and reference preselection Key point limit 40,000 and tie point limit 4,000 (default) Manual realignment when required
2. Constructing dense cloud	High quality, mild depth filtering Manual cleaning (removing outliers, gap filling)
3. Constructing mesh	3D surface from dense cloud High face count Interpolation enabled Cropping to size
4. Constructing DEM	From mesh Interpolation disabled
5. Constructing orthomosaic	From DEM Hole filling enabled

D.2 Indicator species analysis

Table D.2.1 shows the outputs of the indicator species analysis, displaying which species were associated with each of the four identified assemblages subdivided by trophic group.

Table D.2.1: *Species associated with each cluster, where * indicates significant association.*

	UM_OFF	LM_OFF	UM_AM	LM_AM
Planktivores	*Acanthurus thompsoni** *Chromis fieldi** *Lepidozygus tapeinosoma** *Melichthys indicus** *Odonus niger** *Pseudanthias bimarginatus** *Pseudanthias squamipinnis** *Pterocaesio tile** *Ostorhinchus apogonoides* *Xanthichthys auromarginatus*	*Myripristis chryseres** *Odontanthias borbonius** *Pseudanthias unimarginatus** *Pseudanthias gibbosus** *Symphysanodon sp. ** *Tosanoides sp. ** *Nemanthias carberryi*	*Pseudanthias cooperi** *Cyprinocirrhites polyactis*	*Plectranthias spp. ** *Priacanthus sagittarius** *Grammatonotus sp*
Piscivores	*Caranx melampygus** *Cephalopholis miniata** *Epinephelus multinotatus* *Gracila albomarginata*		*Cephalopholis nigripinnis* *Epinephelus fasciatus* *Variola albimarginata*	*Caranx lugubris*
Invertivores	*Cephalopholis aurantia** *Chaetodon guttatissimus** *Chaetodon kleinii** *Sufflamen bursa** *Zanclus cornutus** *Anampses lineatus* *Cephalopholis spiloparaea* *Hemitaurichthys zoster* *Labroides bicolor*	*Bodianus leucosticticus** *Chaetodon dolosus* *Chaetodon mitratus*	*Apolemichthys trimaculatus** *Coris caudimaculata** *Sufflamen chrysopterum** *Halichoeres iridis* *Hoplolatilus fronticinctus* *Labroides dimidiatus* *Parupenus macronemus* *Pomacanthus imperator* *Pseudobalistes flavimarginatus* *Sufflamen fraenatum*	*Roa spp.**
Omnivores	*Lutjanus kasmira** *Lutjanus bohar** *Lethrinus nebulosus*	*Paracaesio sordidus*		
Herbivores	*Acanthurus tennentii** *Pseudodax moluccanus** *Acanthurus xanthopterus* *Centropyge acanthops* *Centropyge debelius* *Centropyge multispinis*		*Acanthurus dussumieri* *Scarus spp.*	
Carnivores	*Aphareus furca**	*Liopropoma sp. **	*Cephalopholis sonnerati* *Liopropoma lunulatum*	*Scorpaenodes spp. ** *Seriola rivoliana** *Pristipomoides sieboldii*

D.3 dbRDA outputs

Table D.3.1 and table D.3.2 show the outputs of the dbRDA model, respectively displaying the importance of identified axes and which environmental parameters each significant axis represented.

Table D.3.1: *Significance of axes of abundance (a) and biomass (b) models. The first six axes have a significant ($P < 0.05$) influence on the model and eigenvalues > 1.*

a) ANOVA Abundance dbRDA	**df**	**Sum of Squares**	**% variance**	**F**	**Pr(>F)**	**Eigenvalue**
dbRDA1*	1	6.4396	17.72	25.3836	0.001	6.59
dbRDA2*	1	3.8032	10.94	14.9915	0.001	4.07
dbRDA3*	1	2.3393	8.20	9.221	0.001	3.05
dbRDA4*	1	1.6498	4.67	6.5031	0.001	1.73
dbRDA5'	1	0.801	3.85	3.1572	0.029	1.43
dbRDA6	1	0.6025	3.46	2.3748	0.18	1.28
dbRDA7	1	0.4629	1.51	1.8248	0.364	0.56
dbRDA8	1	0.378	1.72	1.4899	0.511	0.47
dbRDA9	1	0.2482	1.00	0.9782	0.813	0.37
dbRDA10	1	0.2225	0.97	0.8772	0.567	0.36
Residual	75	16.475	44.24			
b) ANOVA Biomass dbRDA	**df**	**Sum of Squares**	**% variance**	**F**	**Pr(>F)**	**Eigenvalue**
dbRDA1*	1	5.5205	14.37	21.4439	0.001	5.52
dbRDA2*	1	3.7207	9.68	14.4528	0.001	3.72
dbRDA3*	1	2.7603	7.18	10.7221	0.001	2.76
dbRDA4*	1	1.7389	4.52	6.7546	0.001	1.74
dbRDA5*	1	1.3191	3.43	5.1238	0.001	1.32
dbRDA6*	1	1.0357	2.70	4.0232	0.003	1.04
dbRDA7	1	0.7548	1.96	2.932	0.054	0.75
dbRDA8	1	0.5871	1.53	2.2806	0.23	0.59
dbRDA9	1	0.4169	1.08	1.6194	0.689	0.42
dbRDA10	1	0.327	0.85	1.2704	0.878	0.33
Residual	77	19.8226				

Table D.3.2: *Biplot scores for main axes of abundance model (a) and biomass model (b). Key drivers per axes were broadly consistent between abundance and biomass models*

a) Abundance model	dbRDA1	dbRDA2	dbRDA3	dbRDA4	dbRDA5	dbRDA6
Depth*	**0.859**	0.359	0.034	-0.135	0.017	-0.204
VRM*	-0.460	**0.520**	**-0.404**	-0.236	0.289	-0.044
Coral*	0.175	**0.624**	0.147	-0.277	-0.192	-0.146
Sediment*	**0.496**	-0.278	-0.189	-0.216	0.048	-0.003
MA*	0.353	0.239	-0.008	**0.718**	0.253	-0.134
Proximity index*	-0.387	-0.168	**-0.580**	-0.050	0.121	-0.204
Slope*	**-0.672**	**0.629**	-0.159	0.138	0.110	-0.009
Rubble*	**0.623**	-0.055	0.008	0.141	-0.099	-0.267
Contagion	-0.426	-0.203	0.100	-0.187	**-0.347**	0.058
Site2 (ALDW1)	0.128	0.034	-0.170	-0.136	**-0.451**	-0.329
Site3 (AST)	-0.252	0.324	-0.466	**0.547**	-0.183	0.021
Site4 (ALP)	-0.001	**0.736**	0.181	-0.331	0.418	0.130
Site5 (POI)	-0.089	-0.366	**0.621**	0.125	0.211	-0.444
Site6 (StJ)	0.206	-0.349	0.067	-0.183	-0.056	0.299
Site7 (DES)	0.101	-0.201	-0.130	-0.213	-0.043	0.360
b) Biomass model	**dbRDA1**	**dbRDA2**	**dbRDA3**	**dbRDA4**	**dbRDA5**	**dbRDA6**
Depth*	**0.921**	-0.0841	-0.106	0.081	-0.248	0.041
Slope*	-0.459	**-0.755**	0.233	-0.201	-0.128	-0.007
Shoredist*	-0.436	**0.631**	0.293	0.206	0.278	0.046
MA*	0.409	-0.071	0.017	**-0.804**	-0.062	0.210
VRM*	-0.345	**-0.690**	-0.088	0.100	-0.352	0.255
Sediment*	0.358	0.262	**-0.435**	0.257	-0.017	-0.167
Proximity index*	**-0.519**	-0.126	**-0.486**	-0.042	-0.289	-0.075
Site2 (ALDW1)	0.131	-0.0650	-0.170	0.1343	-0.094	-0.711
Site3 (AST)	-0.225	-0.527	-0.248	-0.510	0.200	-0.169
Site4 (ALP)	0.247	-0.591	0.390	0.235	-0.318	0.389
Site5 (POI)	-0.111	0.586	**0.488**	-0.187	-0.389	-0.065
Site6 (StJ)	0.109	0.361	-0.122	0.319	0.200	0.054
Site7 (DES)	0.021	0.112	-0.183	0.17366	0.380	0.417

D.4 Partial dependence plots

Figure D.4.1 to D.4.4 show partial dependence plots visualising the response of assemblage characteristics (abundance, biomass, Shannon-Wiener diversity and functional (trophic group) richness) to main predictor variables.

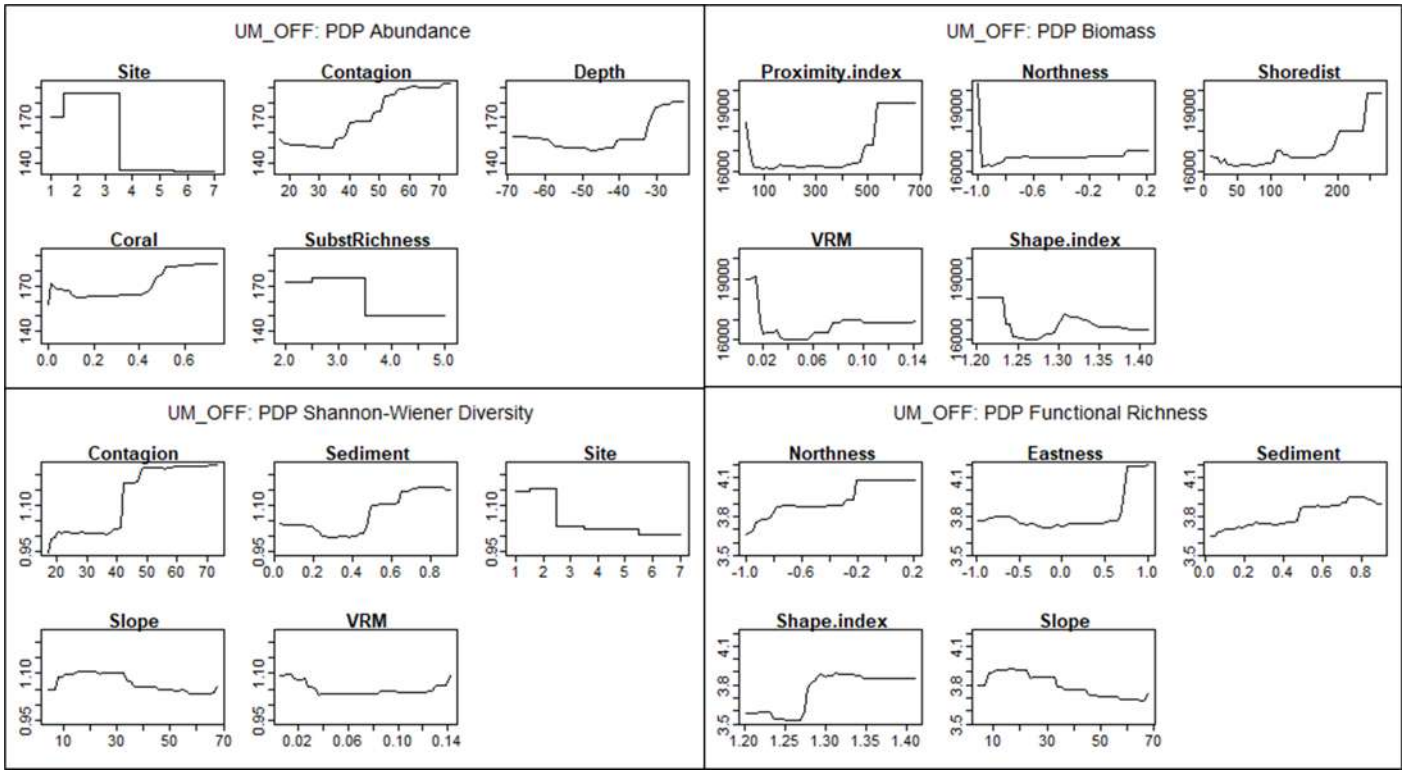


Figure D.4.1: Partial dependence plots of five main contributors to UM_OFF – 30-60 m offshore islands

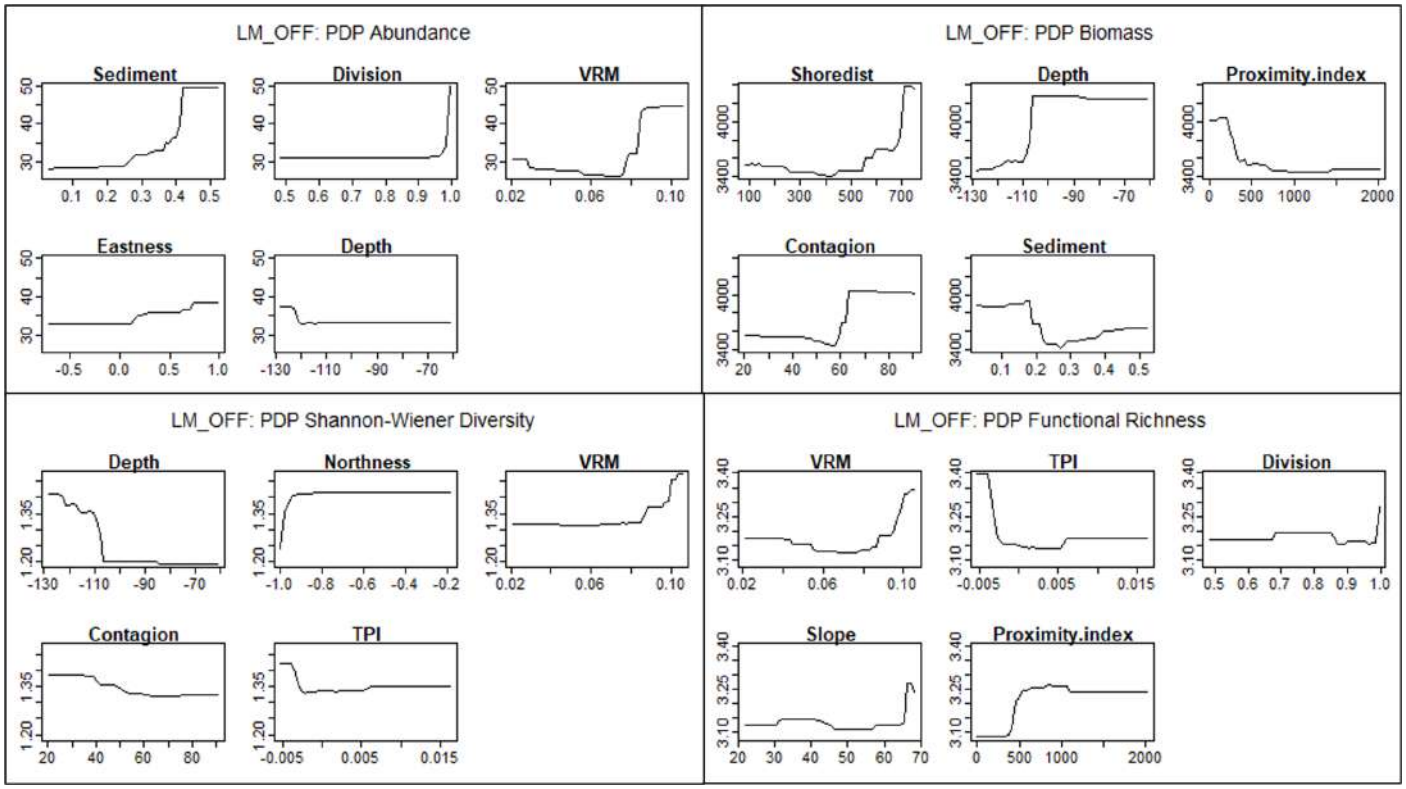


Figure D.4.2: Partial dependence plots of five main contributors to models LM_OFF: 120 m offshore islands

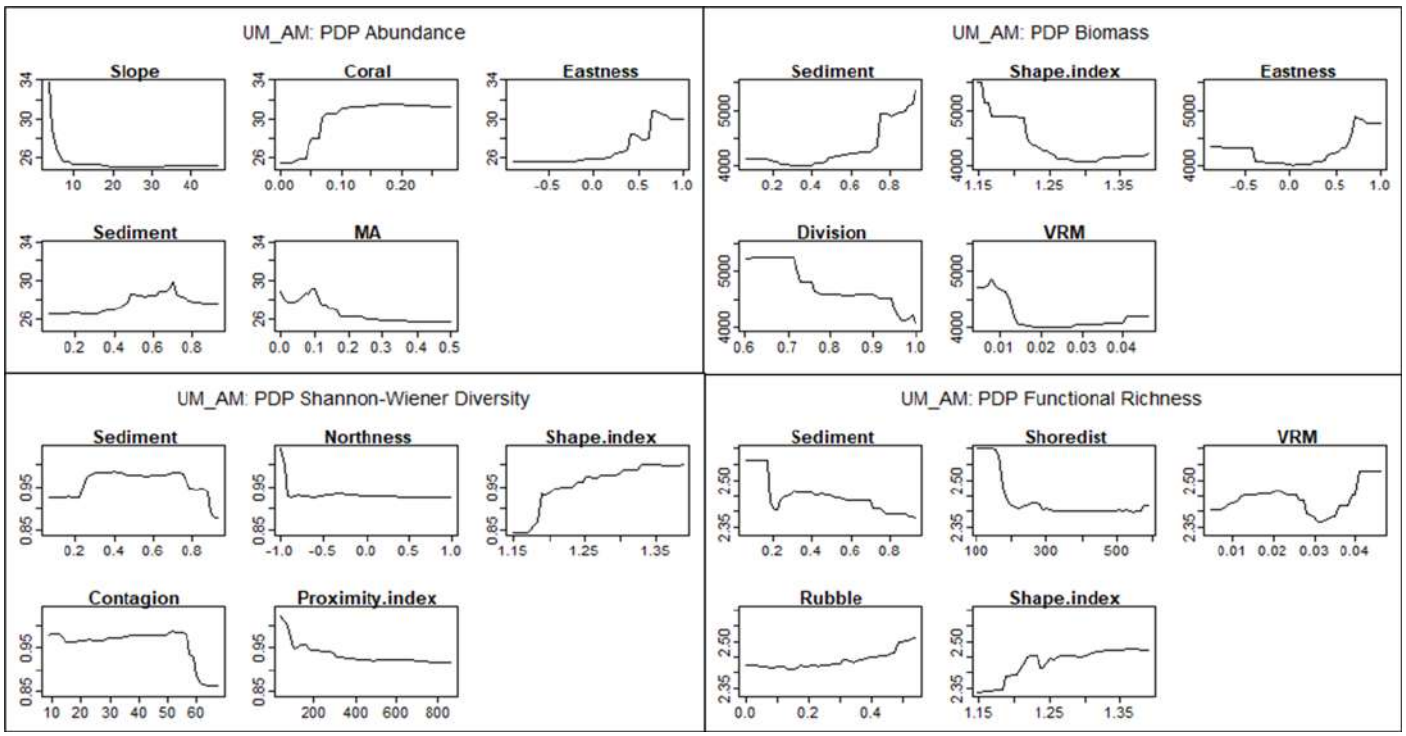


Figure D.4.3: Partial dependence plots of five main contributors to models of UM_AM: 30-60 m mesophotic Amirantes Group

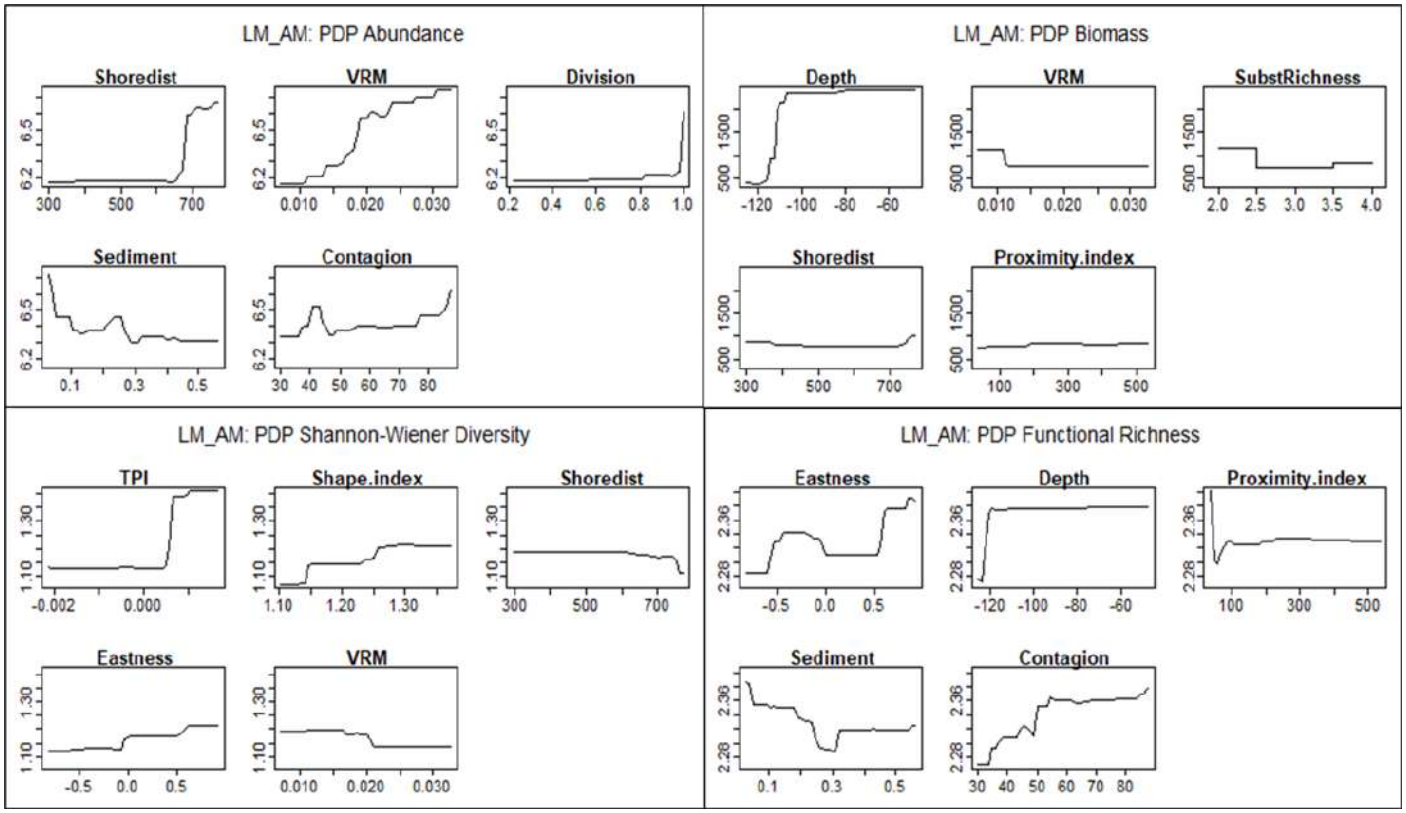


Figure D.4.4: Partial dependence plots of five main contributors to models of LM_AM: 120 m mesophotic Amirantes islands

E Publications resulting from this thesis

E.1 *Bringing seascape ecology to the seabed: a review and framework for its application*

Check for updates

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Bringing seascape ecology to the deep seabed: A review and framework for its application

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Abstract

Seascape ecology is an emerging pattern-oriented and integrative science conceptually linked to landscape ecology. It aims to quantify multidimensional spatial structure in the sea and reveal its ecological consequences. The seascape ecology approach has made important advances in shallow coastal environments, and increasing exploration and mapping of the deep seabed provides opportunities for application in the deep ocean. We argue that seascape ecology, with its integrative and multiscale perspective, can generate new scientific insights at spatial and temporal scales relevant to ecosystem-based management. Seascape ecology provides a conceptual and operational framework that integrates and builds on existing benthic ecology and habitat mapping research by providing additional pattern-oriented concepts, tools and techniques to (1) quantify complex ecological patterns across multiple scales; (2) link spatial patterns to biodiversity and ecological processes; and (3) provide ecologically meaningful information that is operationally relevant to spatial management. This review introduces seascape ecology and provides a framework for its application to deep-seabed environments. Research areas are highlighted where seascape ecology can advance the ecological understanding of deep benthic environments.

The deep ocean is the largest habitat on Earth, representing ~ 66% of the planet's surface area. It provides various ecosystem services crucial to planetary health and societal well-being, including carbon sequestration and storage, nutrient cycling, and the provision of food and energy resources (Thurber et al. 2014). The quality and quantity of ecosystem services depend on heterogeneous and interconnected ecosystems operating across multiple temporal and spatial scales (Levin 1992; Danovaro et al. 2014). Human activities are now a major driver of marine ecosystem change (Halpern et al. 2019), with impacts having reached even the deepest parts of the ocean and capable of modifying the seabed and associated spatial structure of benthic habitats (Puig et al. 2012). A greater understanding of the linkages between the seabed's spatial characteristics, ecological functions, including provisioning of ecosystem services, and the consequences of change is needed to inform ecosystem-based conservation and management plans (Danovaro et al. 2020).

As a result of the logistical challenges of surveying the deep seabed, progress in ecosystem science in the deep sea has advanced less rapidly than in the ocean's more accessible shallow-water coastal regions. However, technological advances in seafloor mapping, ocean observing systems and deep-sea exploration enable a growing scientific interest in studying deep-seabed ecology (Howell et al. 2020). For example, the geographical coverage provided by seabed maps, especially those representing geological characteristics, is rapidly increasing. Global bathymetric data (GEBCO 2021 grid) are currently available at 15 arc-second resolution, with 20.6% of the seabed mapped using echosounders at a spatial resolution of < 100 m (GEBCO Compilation Group 2021). However, scale mismatching between seabed mapping and biological sampling continues to present a challenge. Conventional biological survey methods for the deep sea, such as grab samples or photo/video observations, typically provide point samples or transects covering a relatively small area of seabed, resulting in detailed but geographically and temporally patchy data (Brown et al. 2011). In addition to technical limitations, our

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Author Contribution Statement: DS: Conceptualization; Writing – original draft (lead); Writing – Review & Editing. VH, SP and LW: Supervision; Writing - Review & Editing.

knowledge of spatial patterns and processes has also remained constrained by the conceptual models used to design surveys, formulate research questions, and analyze data.

Although the biophysical environments of deep-seabed and terrestrial landscapes differ, seabed researchers can adapt concepts and tools from other terrain-oriented disciplines such as landscape ecology and geomorphometry to improve comprehension of the ecological effects of seabed heterogeneity (Zajac 2008; Lecours et al. 2016*b*). Seascape ecology evolved from landscape ecology and has led to new ecological insights into structure–function relationships and spatially dynamic processes such as functional connectivity with growing relevance for sustainable management (Pittman et al. 2021). However, unfamiliarity and skepticism of landscape ecology (Manderson 2016; Bell and Furman 2017), social and institutional barriers to cross-disciplinary communication and thinking (Paine 2005), and limited data availability have resulted in relatively slow uptake in marine ecology compared to terrestrial ecology (Pittman et al. 2021). Studies that explicitly draw on the paradigmatic framework of seascape ecology have primarily focused on shallow coastal water areas (Boström et al. 2011; Wedding et al. 2011) (Fig. 1). Yet, environmental heterogeneity is also a key driver of seabed biodiversity and ecosystem functioning at a range of deeper depths,

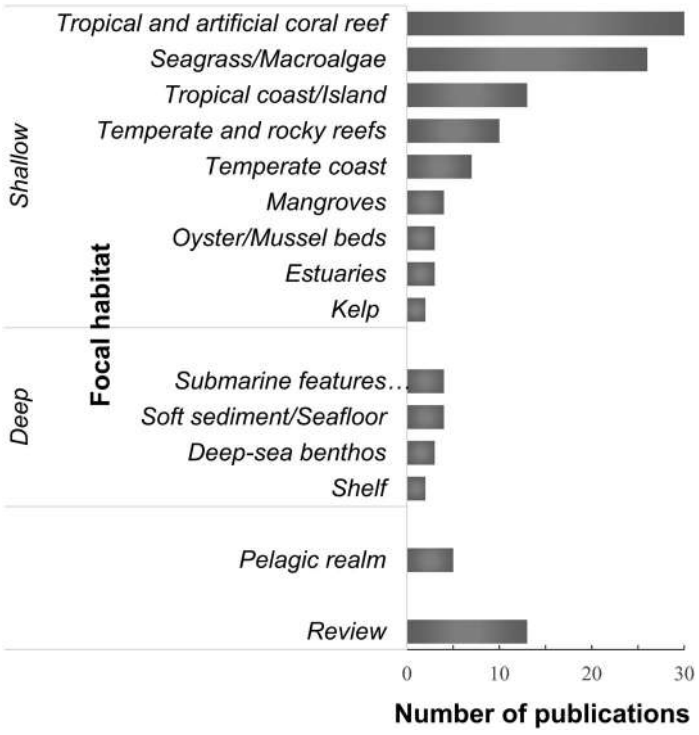


Fig. 1. Google Scholar search (1990–2021) showing peer-reviewed studies that explicitly adopt the terms "seascape ecology," "marine landscape ecology," or "landscape ecology" in combination with "benthic," "seabed," or "seafloor" and classified by focal habitat type. When shallow-water studies incorporated multiple patch types (e.g., seagrass, coral, and mangroves) these were classed under "tropical coast/island."

where seabed terrain models and benthic habitat maps are also widely used to characterize seabed structure (Lecours et al. 2016*b*). Some deep-sea ecologists have started to make progress employing a seascape ecology framework to explore the ecological relevance of spatiotemporal patterns in seascape structure (Teixidó et al. 2002; Zajac 2008; Anderson et al. 2009; Robert et al. 2014; Proudfoot et al. 2020; Price et al. 2021). In several other cases, transfer of landscape ecology concepts to study and provide new insights on habitat heterogeneity and ecosystem functioning has occurred without explicitly citing landscape ecology or seascape ecology as a paradigmatic framework (e.g., Cordes et al. 2010; McClain et al. 2011; De Leo et al. 2014; Durden et al. 2015; Zeppilli et al. 2016).

This review explores the potential of seascape ecology to provide an enhanced pattern-oriented theoretical background and unifying framework to the ecological consequences of deep-seabed structural heterogeneity. The integration of spatial patterns and patterning processes is achieved through a quantitative focus on the key concepts of seascape ecology: composition and configuration, connectivity (horizontal and vertical), context, and consideration of scale (Pittman et al. 2021). Here, we focus on applying seascape ecology to benthic seascapes beyond the depth limits of most non-technical scientific diving and beyond the reach of most air- and space-borne optical sensors (i.e., > 30 m of depth). We discuss the remote sensing techniques most suitable for mapping the deep seabed and the different conceptual approaches (patch-based and gradient models) to model and quantify the structural patterns that characterize the seabed surface as a habitat. Although we recognize these patterns are interconnected with more dynamic pelagic processes in the water column through benthic-pelagic coupling (O'Leary and Roberts 2018), this topic is mostly outside of the scope of the review. We explain how seascape ecology can provide insight into biodiversity patterns and ecological processes through concepts such as spatial heterogeneity, patch composition, configuration and dynamics, topographic complexity, structural connectivity, edges, and the potential for seascape ecology to inform ecosystem-based management using examples from the existing literature. Finally, we highlight priority research areas to advance the study of deep-seabed environments using a seascape perspective.

From landscapes to seascapes in ecology

Landscape ecology focuses on the causes and quantification of environmental heterogeneity—understood as temporal and spatial variation in environmental conditions—and its ecological consequences, considering landscape structure, connectivity, context, and scale (Turner 2005). Importantly, landscape ecology, and therefore also seascape ecology, typically considers multiple scales of interest, often including analyses of spatial patterns at broader scales than other approaches in

benthic ecology. In landscape/seascape ecology, a landscape or seascape is generally understood as "an area heterogeneous in at least one factor of interest," most frequently represented and quantified as a mosaic of discrete internally homogeneous patch types (e.g., habitat patches, biotopes, patch mosaics) or a varying continuous surface (e.g., terrain structure, environmental gradients) (Turner and Gardner 2015). Landscapes are defined not by geographic extent (i.e., there is no such thing as a fixed landscape scale or a landscape level) but rather by the scales(s) that are most relevant to the ecological phenomenon under consideration (Wiens 1989). Over the past 50 years, landscape ecology has become well integrated in mainstream terrestrial ecology, influencing how scientists and practitioners perceive and make decisions about terrestrial landscapes, including protected area design for biodiversity conservation (Turner 2005; Wiens 2009) and potentially serving as a sustainability science (Opdam et al. 2018).

Although landscape ecology has traditionally focused on terrestrial and shallow aquatic systems, its research questions, methodologies, and applications are also relevant to marine systems (Hinchey et al. 2008; Wedding et al. 2011; Bell and Furman 2017). First proposed three decades ago as a way forward in understanding coastal biodiversity patterns (Ray 1991), seascape ecology has gradually emerged as the marine counterpart of landscape ecology to understand the causes, character, and consequences of multiscale spatial and temporal heterogeneity in marine environments (Pittman et al. 2021). Despite significant biophysical differences between land and sea (Steele 1989), concepts developed on land have proven relevant to marine systems, especially in the study of benthic pattern-process linkages and vice-versa (Barry and Dayton 1991; Jelinski 2015; Bell and Furman 2017). Like terrestrial landscapes, benthic seascapes, sometimes referred to as marine landscapes or benthoscapes (Zajac 2008; Proudfoot et al. 2020), can exhibit discrete patchiness and gradients in substrate characteristics and hence in the availability and quality of habitats (Harris 2012; Bell and Furman 2017). In fact, foundational research in landscape ecology around landscape dynamics and disturbance emerged from studies of intertidal ecosystems (Levin and Paine 1974). Seascape ecology, as practiced by benthic ecologists, integrates analytical techniques from landscape ecology, including geomorphology, spatial pattern metrics, multiscale analyses, remote sensing, and habitat mapping to study the ecological relationships between seabed spatial environmental patterns and ecological processes (Wedding et al. 2011; Turner and Gardner 2015; Pittman et al. 2021). Pelagic seascape ecology also draws on biological and physical oceanography (Kavanaugh et al. 2016).

Heterogeneity in seabed environments

Compared to shallow marine systems, few studies in the deep sea explicitly cite the paradigmatic framework of landscape or seascape ecology when studying multiscale categorical or continuous seabed spatial heterogeneity (Fig. 1, including Teixidó et al. 2002; Zajac 2008; Robert et al. 2014, 2016; Ismail et al. 2018; Proudfoot et al. 2020; Price et al. 2021), despite interest in such habitat heterogeneity as a driver of deep-seabed biodiversity and ecological processes (Zeppilli et al. 2016). Like shallow-water environments, the deep seabed exhibits complex environmental heterogeneity in space and time that can be measured in the geology, sediments, topography, hydrodynamic and biogeochemical processes, and other biological activity and disturbances (Table 1). Seabed topography influences exposure to the hydrodynamic regime, modifies sedimentation rates, and shapes substratum characteristics and resulting settlement opportunities across spatial scales (Danovaro et al. 2014). Such heterogeneity influences habitat suitability for species and drives biological distributions, assemblage composition and the local and regional ecology across multiple scales and topographic structures as seeps, canyons, and seamounts may provide priority habitat (Levin et al. 2010; Borland et al. 2021). Dynamic processes in the water column such as currents and boundary layers, internal waves, thermal stratification, and gradients and patchiness in various chemical and biological parameters (Cordes et al. 2010; Kavanaugh et al. 2016) influence seabed habitat through benthic-pelagic coupling (O'Leary and Roberts 2018). The spatial patterning of benthic organisms also creates ecologically relevant biogenic structure on the seabed. For instance, cold-water corals shape distinct patches of structurally complex habitats, embedded in less vertically complex silt and sand sediments on which other animals depend (Price et al. 2021). Structural, chemical, and physical disturbance effects, including direct human activities such as trawling and mining, further modify benthic seascape structure (Table 1). For example, fisheries trawling activity can physically damage or fragment biogenic patches formed by cold-water coral, altering habitat quality and availability sometimes with very low recovery rates (Puig et al. 2012; Huvenne et al. 2016). Seabed heterogeneity also influences the spatial patterning and rates of sedimentary biological processes that influence carbon sequestration and storage at the seabed, with implications for climate regulation (Snelgrove et al. 2018).

A seascape ecology framework for benthic seascapes

This review discusses the key conceptual and methodological attributes of a seascape ecology framework to study deep benthic seascape heterogeneity and its ecological consequences (Fig. 2). The first step is to develop research questions, which will drive data collection methodology and the evaluation of existing data types, including data quality, and careful consideration of spatial and temporal resolution(s) and extent(s). Important information sources are remote sensing data and statistical models (*see* "Sensing the seabed" and "Mapping seabed habitats for ecological studies"), to produce spatial models of seabed structure representing environmental and ecological heterogeneity. These are typically in the form

Table 1. Examples of drivers of environmental heterogeneity in deep benthic seascapes.

Type	Driver	Influence on the benthic seascape	Example
Geographic	Latitude Longitude Shallow to deep gradients	Regional geological history and environmental gradients	Latitudinal, longitudinal and shallow-deep gradients of marine species richness (Gray 2001)
Topographic	Topography/landform	Local environmental factors, flows, disturbances, geomorphic processes	Effect of different seabed morphologies on benthic biodiversity (Zeppilli et al. 2016; Simon-Lledó et al. 2019), the effect of sedimentary environment on community structure (Zajac et al. 2013)
	Geomorphic processes	Transport of organic and inorganic material—erosion, sedimentation	
	Sediment type and structure	Settlement opportunities, burrowing	
Hydrographic	Hydrodynamics/currents	Transport of nutrients/larvae, settlement opportunities	Ecological connectivity (O'Leary and Roberts 2018)
	Water chemistry	Nutrient availability, acidification, salinity	Importance of water chemistry and temperature in influencing octocoral habitat suitability (Yesson et al. 2012), chemical gradients around seep environments (Cordes et al. 2010)
	Temperature	Taxa-specific thermal tolerances	
Biological activity	Competition, predation, mutualism	Influences possible habitat space, food availability and biologically mediated ecosystem functions	Spatial structuring of benthic communities (Teixidó et al. 2002; Price et al. 2021), biologically mediated nutrient cycling (Snelgrove et al. 2018)
Disturbance processes	Dredging, trawling, mining	Structural habitat alteration	Physical and biological impact of trawls on the seabed (Puig et al. 2012)
	Tectonic activity/sedimentary disturbance regime	Structural habitat alternation	Effects of sedimentological processes on benthic ecosystems (Fontanier et al. 2018)
	Climate change	Ocean acidification, warming temperature, hypoxia, nutrient loading	Anthropogenic and climate change effects on the deep sea (Ramirez-Llodra et al. 2011)

of a patch mosaic or spatial gradients of environmental conditions (e.g., classified habitat maps, terrains) or a combination of both, depending on the question and phenomenon under consideration. Environmental structure in these maps and models can be quantified using spatial pattern metrics appropriate for the question and the relevant spatial construct ("Representing and quantifying seascape patterns"). Through statistical analyses, pattern–pattern relationships and pattern–process relationships can be explored and tested based on core seascape ecology concepts of composition and configuration, connectivity, and context at a range of spatial and temporal scales ("From spatial patterns to ecological processes"). Finally, the results are interpreted, evaluated, and applied to the research question.

Sensing the seabed

Geospatial mapping technologies

Geospatial mapping technologies provide the primary data to generate seascape maps from which seascape patterns can be analyzed. Therefore, selecting appropriate mapping tools and survey strategy is key in seascape ecology and should be guided by the question under consideration and desired outputs, the scale of analysis, and available technologies. A variety of remote-sensing platforms and equipment is available to actively or passively survey seabed structure and is increasing the production of reliable seabed maps in the form of digital bathymetric models and georeferenced images (Fig. 3).

The majority of global ocean bathymetry data sets are constructed from satellite-derived gravity data (radar altimeter measurements), providing a relatively coarse scale (km^2) approximation of seabed terrain structure. Rather than resolving ocean depth directly, radar altimeters measure the distance between an orbiting satellite and the mean sea surface, which is influenced by gravity anomalies associated with topographic features of the seabed (Wölfl et al. 2019). In the coastal zone, satellite-derived bathymetry is becoming a cost-effective technique to obtain high-resolution bathymetry to depths of up to 70 m in clear water by establishing a mathematical relationship between the surface reflectance

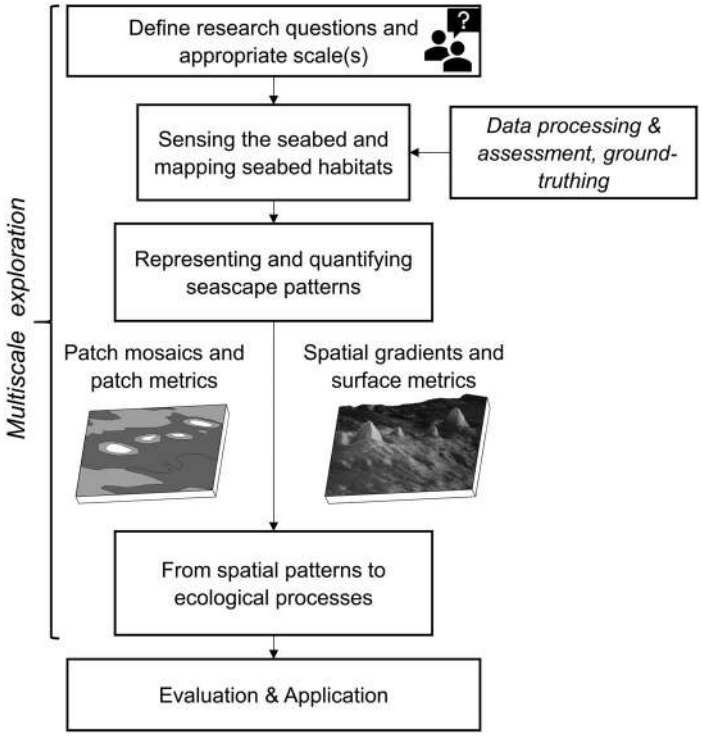


Fig. 2. Example of the logical sequence of steps in a seascape ecology approach to study benthic seascapes in the deep sea.

of shallow waters in specific bands of the visible and infrared spectrum and depth. Satellite-derived bathymetry modeled with geographically weighted regression has been used to identify ecologically important seascape features across shelf ecosystems (da Silveira et al. 2020). Satellite (ICESat-2) and airborne laser altimetry (light detection and ranging [LiDAR]) is also revolutionizing shallow-water bathymetric mapping, but these techniques are typically limited to 30–50 m depth in optically clear water (Lepczyk et al. 2021).

Acoustic mapping technologies such as multibeam echosounders (MBES) and bathymetric side-scan sonar are the main methods to acquire bathymetric data representing the spatial distribution of seabed depth. These acoustic mapping techniques can acquire considerably higher spatial resolution bathymetry than satellite altimetry and passive optical sensors. Sonar has proven particularly useful for seascape ecology studies linking bathymetric complexity to other surficial characteristics (e.g., substratum type from acoustic backscatter) and biological distributions in deep waters (Wilson et al. 2007; Lecours et al. 2016*a*).

Acoustic and optical sensors may also be mounted on autonomous underwater vehicles (AUVs), remotely operated vehicles (ROVs) or human-occupied vehicles (HOVs) for high-resolution mapping of seabed and water column structure including biota (Fig. 3). For mapping purposes, underwater vehicles are most commonly equipped with MBES (Robert et al. 2017), but subsea LiDAR systems rated to depths of over 3000 m are now also becoming available (Filisetti et al. 2018). Seascape studies surveying fine-scale characteristics of the seabed are also increasingly adopting photomosaics, stereo-photography and structure-from-motion (SfM) photogrammetry to map the seabed at sub-meter scale using cameras mounted on underwater vehicles. These cost-effective image processing techniques are particularly useful for investigating fine-scale (millimeters to meters) linkages between terrain structure and biodiversity, even on vertical seafloor terrain (i.e., steep banks and canyon walls; Robert et al. 2017; Price et al. 2019, 2021).

Biological data collection and image processing

Although geospatial mapping tools can provide broad-scale and continuous information on bathymetry and other indirect measurements of seabed structure, used in isolation they often lack biologically detailed information about the seabed required for ecological studies. When available, detailed and georeferenced in situ observations on biological components (species and assemblages) and abiotic

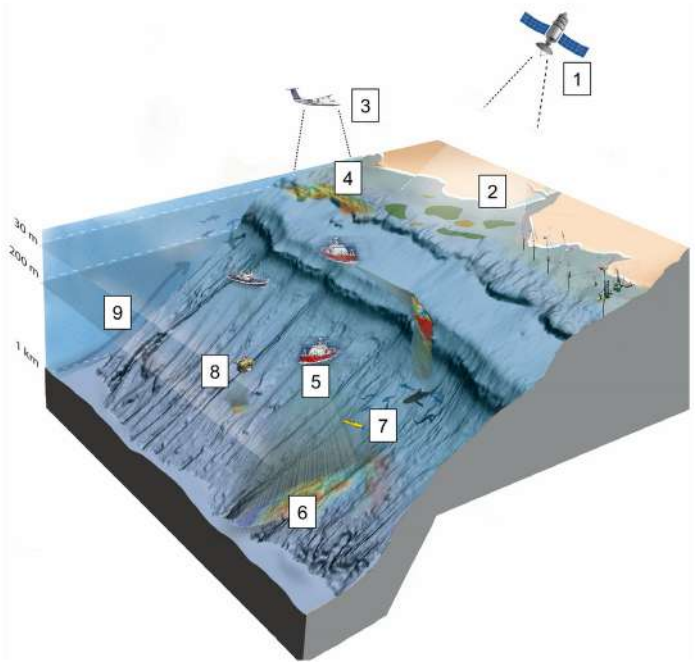


Fig. 3. A growing number of sensors, deployed both above and underwater, are available to map seabed structure. Sensors produce data with different spatial characteristics and depth limits. Satellite data (1) can be applied to map patch-based structure (2) of shallow-water environments (down to 30–50 m depth) and to create satellite-derived bathymetry. Air- and space-borne LiDAR (3) can produce accurate bathymetric data (4) of coastal shelf environments (30–50 m depth). Ship-mounted SoNAR (5) provides information on the continuous 3D structure of deeper seabed environments and slope environments at varying resolution and greater depths (6). At the finest scales, underwater AUVs (7) and ROVs (8) may be applied to map seabed structure (cm^2–m^2 resolution) using sonar and optical approaches such as subsea LiDAR and photogrammetry. Some water column patterns and processes relevant to seabed ecology can also be mapped with remote sensors such as currents, internal waves and stratification (9).

characteristics (substratum type, geology) are extremely valuable, even if geographically sparse. Methods available to obtain ground-truthing on ocean ecology and environmental conditions, including grabs, cores, and nondestructive underwater video observations, have been reviewed elsewhere (Woodall et al. 2018; Danovaro et al. 2020). Here, we highlight underwater vehicle-mounted georeferenced benthic video and photography as a nondestructive technique to collect georeferenced deep-seabed observations. Camera systems can be deployed using stationary (e.g., drop cameras or landers) and mobile platforms (e.g., ROV or AUV), and mobile image data are typically collected in the form of a transect. For all platforms, a system to record geographic position (e.g., ultrashort baseline or estimation from vessel Global Positioning System (GPS)), is crucial to link observed biodiversity and environmental conditions. Spatial scaling can be obtained through laser scales, exact measures of the camera set-up, or through stereo image systems. The annotation process extracts physical, biological, and ecological data of interest such as taxonomic presence and absence, diversity and biomass, animal behavior, sediment type, and habitat structure. When accurate identification is not possible, species observations are recorded as morphospecies or morphotype, and international efforts are emerging to develop common standards and reference guides to identify marine morphotypes (Howell et al. 2020). Advances in marine visual imaging have greatly increased the efficiency of data collection from marine surveys, and significant developments continue in computer vision and automated classification (Durden et al. 2021).

Mapping seabed habitats for ecological studies

A key challenge in seabed ecology is the scale discrepancy between the capability to measure (1) spatially continuous measures of the physical aspects of the seabed (i.e., bathymetric surveys); (2) comparatively fine-scale biological point samples and transect data (photos, videos, grabs, cores); and (3) the scale(s) relevant to the ecological processes under investigation. Benthic habitat mapping combines environmental data sets reflecting seabed topography (bathymetry) and substratum type (using the strength of acoustic backscatter as a proxy) and, when available, in situ ground-truthing of biology and seabed characteristics. Using multiscale terrain derivatives as spatial proxies, surrogates or indicators of species, and habitat distributions, seabed habitat mappers aim to produce spatial representations of the potential occurrence and distribution of seabed habitats (Brown et al. 2011). A seabed habitat is an area defined by physical, chemical, and biological parameters that may correspond to environmental preferences of a species or group of organisms at particular temporal and spatial scales (Lecours et al. 2015). Parameters in the overlying water column that structure seabed habitat distribution may also be sampled by sensors (e.g., acoustic Doppler current profiler) or estimated through physical models (Pearman et al. 2020).

Habitat maps in their many forms are enabling tools in seascape ecology, as they visually represent spatial patterns and provide an opportunity to quantify seascape structure at multiple scales. There are three main habitat mapping approaches for deep-seabed environment that display biological

Table 2. Habitat mapping approaches in deep-seabed environments and selected applications.

Mapping approach	Output	Seascape ecology relevance	Examples
Top-down habitat mapping	Discrete classification into areas of similar environmental characteristics corresponding to potential habitats	Classification of seabed surface morphology that allows for quantification of terrain composition and configuration (2D)	Submarine Canyon habitat characterization (Ismail et al. 2015), MPA prioritization (Hogg et al. 2016), and coastal habitat and substratum characterization (Shumchenia and King 2010; Calvert et al. 2015)
Bottom-up habitat mapping	Discrete classification into potential habitat patches incorporating ground-truthing data	Classification of habitat types allowing for characterization of composition and configuration (2D) Characterization of ecology–environment relationships	Distribution of benthic habitats on fishing ground (Buhl-Mortensen et al. 2009), sponge and coral habitats (Neves et al. 2014) and coastal habitats and substratum (Shumchenia and King 2010; Calvert et al. 2015)
Spatial predictive mapping	Continuous probability distribution of species or habitats	Characterization of species–environment relationships (2D/3D) and resulting distribution, filling geographical knowledge gaps	Distribution of cold-water corals (Ross and Howell 2013; Robert et al. 2016)

distributions as categorical classes or continuous probability distributions (Brown et al. 2011) (Table 2).

Top-down and bottom-up habitat mapping

Top-down and bottom-up habitat maps both segment the seascape in categorical classes representing seabed habitats but differ with respect to the inclusion of ground-truthing data. Top-down habitat mapping (unsupervised approaches, marine landscape mapping or abiotic surrogate mapping) has developed as a response to limited biological data in offshore environments (Verfaillie et al. 2009). It relies on segmentation and classification methods to identify patterns in seabed attributes and discriminate between potential habitats, traditionally covering large areas lacking biological data. This approach assumes that the same factors that shape environmental patterning shape habitats (Shumchenia and King 2010) and outputs show the distribution of spatially discrete areas classified as patch types and potential habitats. Environmental characteristics (lithology, relief, grain size, bedforms, and geological history) distinguish habitat types (McArthur et al. 2010). Top-down approaches are particularly useful for seascape studies where ground-truthing data are absent or discontinuous and have, for example, been used for the characterization of seascape structure (Ismail et al. 2015) and the design and evaluation of potential Marine Protected Areas (MPAs) (Hogg et al. 2016). When available, biological data may be used to classify and ground-truth the map post hoc and assess its ecological relevance by modeling biological characteristics against map units or classes (Hogg et al. 2018).

Bottom-up habitat mapping (supervised approaches) integrates ground-truthing data in the segmentation and classification process, rather than applying it post hoc. Biological ground-truthing data, for example, are first organized in classes corresponding to assemblages or community types using clustering (Shumchenia and King 2010), ordination (Buhl-Mortensen et al. 2009) or hierarchical habitat classification schemes (Calvert et al. 2015). Community–environment relationships are then used to segment continuous environmental variables in distinct map units representing potential habitat class occurrence and distribution. Ground-truthing data may also take the form of substratum characteristics used to map the distribution of discrete substratum types as a function of geomorphological characteristics (Neves et al. 2014). An appropriate definition of classes (thematic resolution) is essential as the classification type can influence map outcomes (Strong et al. 2019). Machine learning algorithms (e.g., Random Forests, Boosted Regression Trees, Artificial Neural Networks, Support Vector Machines) have advanced the accurate classification of benthic seascapes and can be very effective even in data-poor regions with limited ground-truthing data (Turner et al. 2018).

Spatial predictive mapping

Spatial predictive mapping or distribution modeling approaches produce continuous probability data on the occurrence and distribution of the species or habitat of interest (Elith and Leathwick 2009). Distribution models (DMs) are increasingly applied in the marine environment to model and predictively map individual species, habitats, and biological assemblage metrics such as abundance, biomass, diversity, and functional traits across geographical space. DMs help explain the multiple interacting drivers of biological distribution patterns and forecast environmental change consequences (Melo-Merino et al. 2020). At the deep seabed, DMs also offer great potential to address spatial data gaps, but face challenges associated with a limited availability of ground-truthing data and relevant and reliable spatial predictor data. The majority of DMs are correlative, building on species–environment relationships extracted from known occurrence locations and constructed using statistical approaches (e.g., generalized linear models, generalized additive models), machine learning (e.g., Random Forests, Boosted Regression Trees), the MaxEnt package, or multimodel ensemble approaches (Robert et al. 2016). Varieties of these approaches have been applied effectively to seabed environments where much of the application of DM techniques has been to map distributions of cold-water corals where true absence data are seldom available (Robert et al. 2016; Kenchington et al. 2019*a*) (Table 2).

Representing and quantifying seascape patterns

Although deep-seabed researchers have long recognized the importance of seabed habitat heterogeneity (e.g., the combination, abundance and spatial orientation of different geophysical, chemical, and biological habitat types), it is rarely quantified explicitly (Ismail et al. 2018). In seascape ecology, spatial pattern metrics are applied routinely to quantify spatial heterogeneity, monitor and compare seascapes, predict species and diversity distributions, and provide a starting point to relate seascape patterns to ecological processes (Lausch et al. 2015; Pittman et al. 2021). Patch mosaic and continuous gradient representations are the most often used paradigms to quantify patterns from benthic habitat maps and terrain models and are crucial enabling tools for the application of seascape ecology (Wedding et al. 2011; Lepczyk et al. 2021).

Choice of spatial paradigm to represent seascapes

The choice of conceptual framework and associated spatial model(s) of seabed heterogeneity to address research questions is key to the methods and interpretation of results. Patch-based models, conceptually derived from terrestrial vegetation mapping, represent seascapes as a two-dimensional (2D) surface of discrete patches, each with internally homogeneous environmental conditions and typically with sharp patch boundaries (Fig. 4a; Forman 1995; Cushman and McGarigal 2008). Patch-

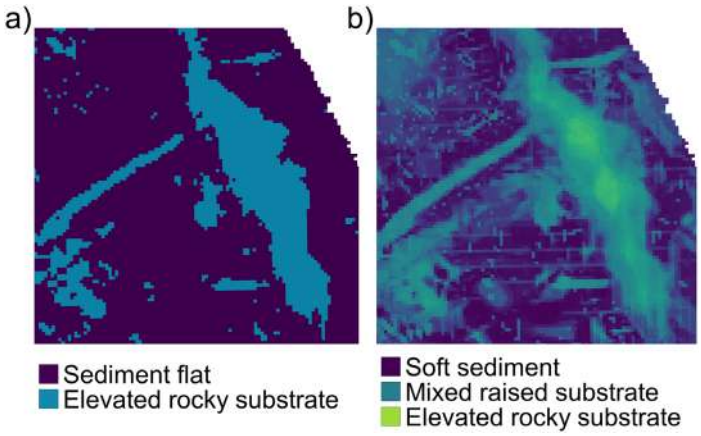


Fig. 4. Patch-mosaic (**a**) and continuous gradient (**b**) representations of seascape structure produced using bathymetry collected around Aldabra atoll, Seychelles, between 150 and 500 m depth. The patch mosaic representation homogenizes within-patch variability and enhances discrete edges, while the gradient model preserves the continuously varying heterogeneity across the seascape.

based models have been applied widely in ecology and have been central to applications of the Theory of Island Biogeography and landscape ecology (Lausch et al. 2015). In benthic environments, categorical or thematic habitat maps are typically either patch-matrix or patch-mosaic models. The patch-matrix model represents focal habitat patches as embedded in an "inhospitable matrix" that is likely to spatially constrain some ecological processes such as individual animal movements of habitat type specialists (e.g., obligate reef species). Patch-matrix theory has for example been used to discuss the theoretical importance of rocky patches in sedimentary abyssal environments (Riehl et al. 2020) and may serve to elucidate metapopulation dynamics, with appropriate habitat patches functioning as "sources" and "sinks" driving the dispersal, assembly, and diversity of species and populations (Puckett and Eggleston 2016). The patch-mosaic model emphasizes that the composition (amount and variety of patch types) and spatial configuration (spatial arrangement of patches) of the seascape unit as a whole influences ecological functioning (Wiens et al. 1993). The patch-mosaic model is an important paradigm for explaining local biodiversity in deep-sea benthos, with patches of environmental characteristics such as substratum, disturbance, and nutrient availability jointly controlling biodiversity (Grassle 1989). However, many benthic systems, most notably soft-sediment terrains, also exhibit spatial gradients and ecotones in seabed characteristics and environmental conditions (Zajac 2008; Brown et al. 2011; Kågesten et al. 2019). Fuzzy classification recognizes that benthic habitats are separated by transition zones or transient boundaries rather than sharp edges (Lucieer and Lucieer 2009; Lecours et al. 2015). Although intuitive, the patch-mosaic model may hinder the ability to detect species' responses to such gradients of heterogeneity (McGarigal and Cushman 2005).

In contrast, the spatial gradient or continuous surface model has been advanced in landscape ecology as an alternative to patch-based models (Fig. 4b) and represents seascapes as continuously varying surfaces without discrete patch boundaries (Wedding et al. 2011). The gradient model avoids the homogenization of potentially important within-patch complexity and the problem of ecologically arbitrary classification that can occur in categorical habitat classifications (McGarigal and Cushman 2005; McGarigal et al. 2009). The gradient model recognizes that many organisms and ecological processes respond to a gradual multiscale variation in spatial heterogeneity, consistent with niche-based gradient theory (McGarigal and Cushman 2005). For example, a study in seep environments demonstrated macrofaunal abundance and diversity responded to gradients of chemical conditions (methane fluid flow) in addition to biogenic patch character (Cordes et al. 2010). With 2.5D digital bathymetric models being the primary data layer to study seabed structure, continuous gradient models are already routinely applied in seabed environments to produce habitat maps and DMs by applying surface metrics from marine geomorphometry (Lecours et al. 2016*b*). Increased application of fine-scale survey techniques such as laser scanning and photogrammetry to seabed environment also enables the construction of true volumetric three-dimensional (3D) reconstructions of continuous seascape structure (Lepczyk et al. 2021). 3D representations may capture additional ecologically relevant aspects of seascape structure and have been used in the deep sea to quantify surface area covered by cold-water coral (Fabri et al. 2019).

Whether to represent seascapes as continuous gradients of environmental and biological conditions or as patch-matrix or patch-mosaic depends on the research question's conceptual framework, data availability and quality, and the ecological phenomenon under consideration (McGarigal et al. 2009; Wedding et al. 2011). Both patch-based and gradient model approaches have successfully been applied to understand biophysical drivers of habitats and species in the marine environment (Ferrari et al. 2018). Because both patch-mosaic and gradient models represent ecologically relevant patterns, an integrated patch-gradient model framework that includes individual metrics derived from both models can offer further insight into ecological consequences of environmental heterogeneity (Sekund and Pittman 2017). Models predicting coral reef fish distributions in Hawaii that combined 2D and 3D explanatory variables outperformed models with only 3D or 2D variables (Wedding et al. 2019). Likewise, in deep water across Cordell Bank in California, demersal fish responded to discrete patchiness and patch context across continuous gradients in seabed terrain character (Anderson et al. 2009).

Spatial pattern metrics for quantifying seabed heterogeneity

A wide range of metrics are available for quantifying the spatial structure of the seascape represented in either a patch-

based or gradient model (Frazier and Kedron 2017) (Table 3) and computing tools are available to aid multiscale analyses (McGarigal et al. 2012; Walbridge et al. 2018).

Patch-based metrics can be categorized broadly into composition (i.e., number of patch classes and their abundance in the seascape) and configuration (i.e., spatial arrangement, orientation, and shape of patches in the seascape). In addition, they can be applied at different levels of structural organization to quantify attributes for (1) individual patches, (2) patch classes (all patches of the same type) or (3) an entire seascape unit (i.e., measures of seascape composition and configuration) (Gustafson 2019). Patch metrics enable researchers to quantitatively explore and describe the spatial structure of the benthic environment at a wide range of depths and spatial scales. For example, patch size and variability, patch diversity, and patch interspersion emerged as key variables to characterize the fine-scale (1 m^2) spatial patterning of Antarctic benthic communities (Teixidó et al. 2002). At broader scales, spatial configuration metrics including contagion (clumping of attributes) functioned as a spatial proxy for biodiversity when comparing the spatial heterogeneity among branches of a submarine canyon (Ismail et al. 2018). Patch metrics also have specific applications in understanding the effect of seabed patterns on the distribution of species and the composition of species assemblages including structure, richness, and diversity. In the Cape Howe Marine National Park (Victoria, Australia), seascape composition and configuration combined with depth explained 35% of variation in demersal fish assemblage, indicating that combinations of both patchy and contiguous habitats maximize fish diversity and abundance (Moore et al. 2011).

Despite their demonstrated ecological relevance, patch-based metrics have found limited application in explaining the functional relevance of heterogeneity observed across deep-seabed environments compared to shallow-water environments (Robert et al. 2014; Ismail et al. 2018). Marine geomorphometry methods and metrics are more widely applied to describe and analyze deep-seabed spatial patterns from digital bathymetric models, and are readily accessible in common GIS software and open-source statistical computing code (Lecours et al. 2016*b*; Lucieer et al. 2018). Geomorphometrics (also referred to as terrain metrics or surface metrics), measuring slope, orientation, curvature, and terrain complexity, have been identified as key drivers of seabed biodiversity patterns and ecological processes over multiple scales (Wilson et al. 2007; Brown et al. 2011; Bouchet et al. 2015). For example, terrain slope has been used as a key predictor of global habitat suitability and distribution for six orders of cold-water octocoral (Yesson et al. 2012) and to identify elevational gradients associated with high megafaunal biodiversity in abyssal environments (Durden et al. 2015). Working with continuous gradients offers analytical flexibility, including greater opportunity for creating derivative metrics (e.g., range, maximum, minimum, standard deviation), multiscale analyses and capturing emergent ecological properties of multiple metrics (McGarigal et al. 2009). DM outputs can be interpreted as continuous habitat suitability surfaces (McGarigal and Cushman 2005), from which patterns can be quantified and incorporated in further ecological analyses. For example, a study around Hoburgs Bank in the Baltic Sea demonstrated that continuous probability maps of seabed substratum and biodiversity were valuable inputs for further benthic classification such as applying thresholds (Kågesten et al. 2019). Although predicted patterns from DMs are rarely explored with pattern metrics, additional analysis and examination of ecological implications is an interesting area for future research attention.

Regardless of the choice of conceptual model and associated metrics, key considerations for the selection of spatial pattern metrics should be their ecological relevance as driver or proxy (Kupfer 2012) of the phenomenon under consideration (Lecours et al. 2016*a*), the sensitivity of the data to interpretation rules and interdependencies, and any redundancy of indices (Turner 2005; Cushman et al. 2008). In metric extraction, researchers should consider neighborhood sizes and temporal, spatial, and thematic resolution of mapped data, scale-dependent effects on pattern metrics that may influence the results of ecological analyses, as well as error propagation (Kendall et al. 2011; Moudrý et al. 2019). To facilitate comparative studies and robust interpretations of the seabed and associated biological communities, researchers should explicitly address their methodology in choosing terrain metrics and extracting them, the ecological rationale behind scales chosen and analysis techniques (Lecours et al. 2016*b*). Regardless of the metrics applied, the choice of statistical technique can influence spatial predictions. Robert et al. (2016) identified technique-specific predicted patterns in habitat suitability for cold-water coral species assemblages on the Rockall Bank (NE Atlantic) when comparing results from multiple techniques and with highest performance achieved with an ensemble of all model outputs.

As seabed habitat suitability and species distributions are strongly influenced by dynamic temporal and spatial heterogeneity in the overlying water masses, for example in the form of current exposure, water chemistry, nutrient concentration and tidal regimes (Yesson et al. 2012), seascape metrics of seabed characteristics alone are unlikely to explain all biological variation. Therefore, an important future focal area in seascape metric research is developing and integrating pelagic metrics measuring continuous structure and patchiness in the overlying water column, for example, from remotely sensed satellite data or physical models (Kavanaugh et al. 2014; Alvarez-Berastegui et al. 2016). For example, predictive models incorporating high-resolution hydrodynamic data (baroclinic and barotropic current speed, salinity, temperature) in Whittard Canyon, NE Atlantic, explained more variation in cold-water coral species richness, abundance and diversity compared to models constructed with topographic parameters alone (Pearman et al. 2020).

Table 3. Spatial pattern metrics applied to patch-mosaic and continuous gradient models, with selected examples.

Metric category	Examples of metrics	Measures	Ecological importance	Selected examples
2D—composition	Patch size	The area of each patch	Information on basic area requirements, an indicator for species richness	Composition of Antarctic benthic communities (Teixidó et al. 2002)
	Patch richness	Number of patch types in the landscape	Information on the representation of different habitat types	Quantification of seascape spatial heterogeneity (Ismail et al. 2018)
	Patch proportion or evenness	The proportional abundance of each patch in the landscape	Species richness, habitat fragmentation	Fish–habitat associations and distribution of demersal fish (Moore et al. 2011; Anderson et al. 2009)
	Shannon's or Simpson's diversity index	Landscape diversity—dependent on the number of patches and proportion	Proxy for species diversity, spatial configuration, resilience to disturbances	Distribution and diversity of megabenthic invertebrate communities (Robert et al. 2014, 2016; Zajac et al. 2013)
2D—configuration	Edge to area ratio	Length of edge segments	Proxy for ecological processes through edge effects	Evaluation of structural connectivity (Proudfoot et al. 2020)
	Core area	The patch area away from a buffer zone	Habitat quality	
	Shape index	The geometric complexity of the patch	Seascape complexity, edge effects	
	Contagion	A measure of landscape clumping	Dispersion of landscape, metapopulation dynamics	
	Interspersion and juxtaposition index	A measure of the intermixing of different patch types	Seascape connectivity, dispersal	
	Proximity index	A measure of patch isolation	Seascape connectivity, dispersal	
	Fragmentation index	A measure of landscape splitting in discrete patches	Disturbance to habitat structure	
2.5D—terrain structure	Slope	Elevational change	Local hydrodynamic regime (exposure, food supply), the stability of surface	Production of benthic habitat maps (Hogg et al. 2016, 2018; Ismail et al. 2015, 2018)
	Mean depth	Distance to the ocean surface	Proxy for physical processes including temperature, light penetration, sedimentation	Macrofauna–habitat associations (Durden et al. 2015; Simon-Lledó et al. 2019)
	Aspect	Orientation of surface	Exposure to currents, sedimentation	Predictive distribution of VMEs (Buhl-Mortensen et al. 2009; Yesson et al. 2012; Ross and Howell 2013; Robert et al. 2016; Pearman et al. 2020)
	Seascape curvature (e.g., curvature or bathymetric position index)	Orientation and relative elevation of the surface	An index measuring exposure/shelter)	
	Habitat complexity (e.g., rugosity, vector ruggedness measure)	Critical for ecological functions and habitat prediction	Settlement opportunities, microhabitats, shelter from exposure	Species–habitat associations and distribution of demersal fish (Borland et al. 2021)
				Determining hotspots of predator activity (Bouchet et al. 2015)

(Continues)

Table 3. Continued

Metric category	Examples of metrics	Measures	Ecological importance	Selected examples
				Quantification of fine-scale habitat complexity (Price et al. 2019, 2021)
3D—true volumetric	Surface area	Total area that surface of object occupies	Surface area to volume can also function as descriptor of habitat structure	Quantification of reef surface area (Fabri et al. 2019)
	Volume	Three-dimensional space that object occupies		

From spatial patterns to ecological processes

Like terrestrial landscape structure, seabed structure—the abundances, combination, spatial orientation, and variation in geophysical and biological habitat—influences the spatial flows of matter, energy and organisms and other critical ecological processes that shape ecosystem functioning (Barry and Dayton 1991). Therefore, seascape and habitat heterogeneity facilitate, hinder, or constrain key ecological processes such as species dispersal, establishment, resource acquisition, reproduction and metapopulation dynamics, and the horizontal and vertical connectivity between seabed ecosystems. This section introduces how seascape ecology can provide insights into the ecological consequences of seabed heterogeneity through the concepts of (1) seascape structure, comprising composition, configuration and terrain variability; (2) ecological connectivity; (3) seascape context; and (4) scale considerations (Fig. 5).

Seascape structure: The ecological importance of patch mosaics and terrains

Seascape structure, the spatial composition and multidimensional configuration of the seascape, has been the focus of seascape ecology efforts to quantitatively link seascape heterogeneity to biological distribution patterns, organism

Fig. 5. Schematic representation of patch-based seascape structure at the seabed, based on the patch-matrix model. Seascapes differ in the composition and configuration of habitats (**a**), such as their size and shape, which influences processes as connectivity in the seascape (**b**). The surrounding environment (**c**) has further effects on ecological flows within the seascape under consideration.

movements, and other ecological processes (Wedding et al. 2011; Pittman et al. 2021). From a seascape ecology perspective, seascape structure comprises three main concepts: (1) composition (the variety and relative abundance of patch types); (2) spatial configuration (the spatial arrangement of patches); and (3) terrain structure (variations in seabed depth) (Fig. 5a), which all are measured using spatial pattern metrics applied to habitat maps and/or terrain models (Table 3).

In shallow-water systems, studies relating seascape structure to marine organisms through spatial pattern metrics have successfully generated new insights on species-specific responses to seabed heterogeneity (Boström et al. 2011), structure-mediated animal movement behavior (Hitt et al. 2011), the effects of seasonality and life stage (Staveley et al. 2017), predator–prey dynamics (Hovel and Regan 2018), and the genetic structure of marine species (Van Wynsberge et al. 2017). Understanding the implications of seascape structure for the distribution of species and habitats and ecological processes is equally of interest to deep-seabed ecologists, with habitat heterogeneity a long recognized key research topic (Grassle 1989; Levin et al. 2001). Important knowledge gaps remain about patch size, patch spacing and crucially, the drivers and implications of such spatial patchiness (Kaiser and Barnes 2008; Cordes et al. 2010). Seascape ecology can contribute to addressing these knowledge gaps through assessing the potential effects of seascape composition, configuration, and terrain structure (Harris 2012).

Seascape composition

Considering the effects of seascape composition, focusing on the size, abundance, and diversity of patches represented in habitat maps, is key to understanding the types, diversity, richness, and abundance of assemblages that the seascape may support (Turner and Gardner 2015). In terms of size, studies in terrestrial systems indicate that larger habitat patches can support more abundant and biodiverse assemblages because within-patch environmental variability increases with area (Harris 2012). Patch size effects have also been examined in deep-sea environments. For example, underwater camera surveys examined the abundance of marine species living on glacially deposited rocks ("dropstones") of varying size, which form distinct habitat patches in a more homogeneous seascape (Ziegler et al. 2017). Relating patch size to assemblage characteristics, the study concludes that dropstones form local biodiversity hotspots with diversity and abundance of organisms predictably increasing with dropstone size following the Theory of Island Biogeography. It is well understood that the diversity of habitat classes shapes biological assemblages. For example, abyssal patches of rocky substratum host different benthic communities than the surrounding sedimentary environment (Riehl et al. 2020). Accounting for the diversity of patch types (e.g., soft sediment, rock, boulders) and broad-scale zones (e.g., slope, bank or shelf) is important in determining the presence, diversity, and abundance of mobile species that use more than one type of habitat during their life cycle (Anderson et al. 2009).

Seascape configuration

Seascape configuration, the shapes of habitats and their physical arrangement in the seascape, adds to seascape composition to influence ecological processes. It can provide insights into habitat suitability and patches' capacity to function as a connected network. Evidence from shallow coral reef ecosystems demonstrates that the configuration of patch types across seascapes influences species distributions and the structure of biological assemblages. For example, the proximity of mangrove habitat to seagrass habitat strongly influenced fish density by facilitating resource availability and organism movement (Pittman et al. 2007; Berkström et al. 2013). Configuration has also been linked to ecosystem services such as food provisioning and carbon storage, with highly connected seascapes storing larger amounts of organic carbon in sediment (Asplund et al. 2021).

Patch shape influences habitat suitability through the availability of core and edge habitat (transition zones between patch types). Because more complex habitat shapes feature a higher proportion of edges, they typically have increased exposure to external disturbances and edge effects. Edge effects, such as exposure to currents and turbidity, create ecotones at patch edges and reduce the availability of core habitat which might disadvantage species dependent on that habitat type (Proudfoot et al. 2020). The study of patch shape provides opportunities for novel scientific questions and investigations such as the implications of disturbance-induced habitat fragmentation. Destructive physical disturbances may lead to habitat fragmentation, with reduced patch size and increased exposure to edge effects, compromising the capacity to support the originally present assemblages. Through exposure to currents and turbidity, the habitat quality of trawled isolated patches of habitat-forming cold-water coral can decrease compared to undamaged cold-water coral habitat, and are therefore less likely to be recolonized by larvae over time, influencing population structuring (Harris 2012).

The suitability of spatial pattern metrics as a spatial proxy in ecological studies of biological assemblage structure has been demonstrated for deep-seabed environments (Table 3). One such study found demersal fish assemblage structure was strongly influenced by the relative proximity and interspersion of benthic habitats into the broader seascape, in addition to focal habitat characteristics (Anderson et al. 2009). On the Rockall Bank, NE Atlantic, spatial composition and configuration of sediment characteristics measured in buffers around biological observations were strongly associated with morpho-species distribution (Robert et al. 2014) and were more important predictors of cold-water coral habitat than measures of terrain structure (Robert et al. 2016).

Measures of seascape composition and 2D configuration applied to habitat maps also offer opportunities to explore

patch dynamics, the changes in patch characteristics over space and time (Levin 1992). The patch dynamics model predicts such changes influence habitat suitability, colonization dynamics, and ultimately population and metapopulation dynamics (Jackson et al. 2018). For example, a study from deep-sea benthos in the Pacific Ocean explicitly recognized the importance of patch dynamics, suggesting that fine-scale dynamic processes as patch extinction and variability, competitive exclusion and variability in carbon supply influence species occurrence and coexistence (McClain et al. 2011). Patch dynamics can be incorporated into a pattern-oriented monitoring tool and has proved useful in terrestrial- and shallow-water change detection and quantifying multiyear changes in Antarctic benthic fauna's spatial patterning (Teixidó et al. 2002).

The above examples demonstrate that patch representations are becoming a promising avenue to quantitatively explore the relationship between multiscale seascape composition and configuration, biodiversity patterns and resulting ecosystem processes. Further research could build on these early examples using patch metrics to study the effect of seascape composition and configuration on processes such as movement behavior and to better understand the patch dynamics of benthic colonization (Proudfoot et al. 2020).

Continuous seascape structure

In some cases, surface metrics are more appropriate metrics or can be combined with patch metrics to capture a broader range of geometric features of the seascape. Continuous seascape structure refers to gradients in environmental conditions, such as terrain structure or habitat suitability, and can be quantified from terrain models or predictive DMs.

Multiscale terrain structure, represented in digital bathymetric models, includes variable gradients such as topographic complexity that may affect habitat suitability through its correlations with substrate quality for colonization, niche space, refuge, hydrodynamic flow characteristics, and nutrient deposition patterns (Pygas et al. 2020). That variations in terrain structure influence the occurrence and structuring of biological assemblages at the seabed has been demonstrated in multiple seabed environments, including in abyssal plains (Durden et al. 2015), continental margins (Levin et al. 2010; Jones and Brewer 2012), banks and seamounts (Quattrini et al. 2017), and at finer spatial scales within cold-water coral reefs (Price et al. 2019). Quantitative measures of continuous seabed surface structure are now routinely applied as spatial predictors in DMs. However, spatial pattern metrics may also be applied to the mapped prediction to quantify the spatial structure in predicted biological distributions and ecological processes. For example, predictive habitat suitability gradients can be used as spatial proxies for modeling processes such as movement behavior or responses to changes in habitat suitability such as habitat fragmentation or loss of structural complexity (Pittman and Brown 2011). Potential exists to use predicted species distribution patterns to examine the geography of functional traits and resulting ecological functions, such as developing spatial proxies for biologically mediated nutrient cycling (Snelgrove et al. 2018). Continuous gradient representations also offer opportunities to quantitatively explore and assess the effect of varying scales on ecological relationships. For example, terrain metrics extracted using moving windows of variable sizes helped identify the scale at which the relationship between cold-water coral diversity and terrain complexity was strongest (Price et al. 2019), and identify species-specific scale-dependent relationships using multiscale models (Pittman and Brown 2011). In seabed environments, DMs using continuous terrain metrics increasingly move beyond explanation and representation of biological patterns. DMs have been used to delineate essential fish habitat, conduct life stage studies and projections of habitat changes (Kenchington et al. 2019*a*), to study genetic variation and adaptation potential (Miller et al. 2019), to inform fisheries management (Stamoulis et al. 2018) and seascape connectivity conservation (Stuart et al. 2021).

Establishing guidelines for selecting patch and gradient metrics for ecological models and at what scale(s) to apply metrics remain important challenges for seascape ecology. Recognizing that both patch-based and gradient spatial pattern metrics have ecologically relevant characteristics, seascape ecologists studying coral reefs have combined metrics from both spatial constructs to model, map, and explain ecological associations finding that a combination of metric types best explains biological assemblages (Sekund and Pittman 2017; Wedding et al. 2019). For the deep seabed too, the value of combining different representations has been demonstrated to study the driving factors of species distributions (Moore et al. 2011; Robert et al. 2014). Furthermore, it is also possible to create patch-based representations from the mapped outputs from geomorphometrics, for example, classes of low to high rugosity (Kågesten et al. 2019).

Ecological connectivity

Ecological connectivity is a central topic in landscape and seascape ecology and refers to the movement of populations, individuals, genes, gametes, and propagules between populations, communities, and ecosystems, as well as that of non-living material from one location to another (Hilty et al. 2020) (Fig. 5b). Connectivity is important for gene flow, maintaining healthy populations and metapopulations, and resilience of ecosystems and populations to disturbance events (Olds et al. 2016). Research into animal movements and genetic connectivity is of increasing interest in the deep-sea research community for its implications for marine conservation and ocean management and has historically focused on cold-water coral, seamount and vent habitats (Taylor and Roterman 2017). Deep-sea connectivity research largely draws on genetic approaches and numerical models of larval dispersal (Hilário et al. 2015; Gary et al. 2020). Challenges remain

in identifying the mechanisms behind seabed population connectivity and their effects due to limited data availability on organism reproductive strategies and movement behavior in the deep sea (Taylor and Roterman 2017).

Few of the deep-sea studies of connectivity draw from landscape ecology and instead emerge conceptually from biological oceanography. However, there remains great potential to adapt approaches from landscape ecologists who often work with models and spatial proxies for variables where insufficient direct data are available. These include using structural connectivity as a proxy to predict actual connectivity pathways (Calabrese and Fagan 2004; Kenchington et al. 2019b) and using graph-theoretic approaches such as network models (Treml and Kool 2017). Connectivity metrics and models quantify ecological connectivity through a focus on either: (1) structural connectivity (i.e., an inference of seascape connectivity from the distribution and spatial properties of physical attributes of the seascape only; Meynecke et al. 2008; Weeks 2017); 2) potential connectivity (i.e., inferring connectivity from seascape attributes combined with limited data on species mobility or dispersal capability; Proudfoot et al. 2020); or (3) actual connectivity (i.e., direct data on movement such as can be acquired with telemetry; Pittman and McAlpine 2003). Structural connectivity approaches consider the location, size, shape, and separation of habitats as habitat fragmentation may predict population spatial dynamics and behavior (Calabrese and Fagan 2004). For example, structural connectivity approaches have successfully linked wetland connectivity to higher fish catch per unit effort, indicating connectivity between coastal habitats positively affects fish stocks (Meynecke et al. 2008). In the deep sea, structural connectivity approaches have demonstrated structural connectivity between 14 closed areas containing vulnerable deep-sea coral and sponge habitat in the North-West Atlantic (Kenchington et al. 2019*b*). Potential connectivity approaches incorporate species-specific dispersal capabilities or physical processes in the overlying water column that influence connectivity (Hilário et al. 2015) and their use in quantifying seabed structure can provide valuable outputs relevant for marine conservation (Proudfoot et al. 2020). Spatial patterns can be used as proxies to estimate the impact of seascape structure on animal movements. For example, in Newman Sound, Eastern Canada, patch size and proximity were used as spatial proxies to model cost surfaces to lobster movement and inform conservation planning solutions (Proudfoot et al. 2020). Actual connectivity research in marine systems incorporates information on measured species-specific movements, such as the dispersal of larvae and post-settlement processes using genetic techniques, models, and markers, further improving the functional relevance of the results (Baco et al. 2016).

Even though major gaps remain in our knowledge of dispersal capacities of deep-sea species, our ability to track animal movements using technologies such as GPS tags, sensors, and acoustic transmitters is increasing, as are capabilities to model animal movements and interpret genetic information (Harcourt et al. 2019). For example, microsatellite DNA revealed that seamounts can function as isolated islands or stepping stones for different taxa and reproductive strategies with implications for designing protected area networks (Miller and Gunasekera 2017).

Connectivity research could also benefit from the application of individual-based models (IBMs). IBMs offer a bottom-up approach to explore the responses of individual organisms and ecosystem variables to simulations of different spatial configurations over a range of temporal and spatial scales (Hovel and Regan 2018). Such experiments are relevant for seabed environments, where the possibility of in situ manipulation of seascape characteristics is limited. IBMs have been integrated with hydrodynamic models to simulate the supply of larvae to coastal nurseries (Rochette et al. 2012). Although IBMs are ideally constructed and validated using in situ data on organism behavior, they can prove useful when estimates are provided (Hovel and Regan 2018). Because of the strong influence of hydrodynamic effects on species dispersal, bentho-pelagic coupling, vertical connectivity between benthic systems, and the influence of terrestrial and atmospheric processes on the deep sea present important focal areas for seascape connectivity studies. Further development of ecologically relevant pelagic spatial pattern metrics quantifying multiscale patchiness and gradients have been proposed to advance the study of vertical connectivity (Kavanaugh et al. 2016).

Context

Seascapes at any scale consist of a hierarchically structured assemblage of habitat conditions connected to, and influenced by, neighboring environments—the seascape context (Fig. 5c). Examples of broader contextual processes influencing the deep seabed include nutrient falls from higher water masses (whales, jellyfish) (Sweetman et al. 2011), sediment deposition from land-based sources (Fontanier et al. 2018) or global heating of the ocean (Danovaro et al. 2020). At finer spatial scales, community characteristics of sediment infauna have been best explained by the characteristics and patch size of nearby cold-water coral reefs (Bourque and Demopoulos 2018). Omitting consideration of spatial context in the study of the structural patterns of a single focal habitat type may therefore fail to elucidate all drivers of biological variation in focal patches and might limit model transferability (Bradley et al. 2020), which is particularly important for data-poor deep-seabed environments.

As patch context influences focal-level processes, ecological models should include both patch variables and patch context. Seascape ecology studies in shallow coastal ecosystems have demonstrated the importance of considering patch context to explain structuring of coastal marine fauna (Grober-Dunsmore et al. 2007; Bradley et al. 2020). Similarly, patch context can likely improve our understanding of the influence of the surrounding environment in deep-seabed focal patches.

A hierarchical seabed survey applying spatial pattern metrics at multiple scales to ROV imagery and sonar-derived data found that accounting for the surrounding (30 and 75 m) spatial context of sediment patches almost doubled the explanatory power of models of variability in morphospecies composition and biodiversity across the Rockall Bank, NE Atlantic (Robert et al. 2014). Likewise, broad-scale (km) and fine-scale (1–10 m) demersal fish-seabed habitat associations were found to be strongly dependent on habitat context, and the surroundings of habitat types contained distinct fish assemblages (Anderson et al. 2009).

Scale

The processes responsible for environmental heterogeneity operate across temporal and spatial scales, and individuals, life-stages, species and communities respond to habitat patterning differently across these scales (Wiens 1989; Turner and Gardner 2015; Martin 2018). The concept of scale covers two aspects: resolution and extent, which can be both temporal and spatial. Secondly, scale consists of a thematic scale (i.e., the number of habitat classes and how they are defined), an ecological scale (i.e., scale of a phenomenon), an observational scale (i.e., the scale at which data is collected) and an analytical scale (i.e., the scale at which data on the phenomenon is analyzed). The selection of spatial and temporal extent(s) and resolution(s) can therefore have profound implications for the capability to successfully link pattern to process (Levin 1992; Wu 2004; Kendall et al. 2011; Lecours et al. 2015), as mismatches between ecological scale, observational scale and analytical scale might compromise the ability to define biota-environment relationships accurately (Holland et al. 2004). The challenge of linking spatial patterns to ecological processes over multiple scales and identifying the most influential scales (scale of effect) has been and continues to be a focal area of landscape ecology (Wiens 1989; Levin 1992; Martin 2018).

Temporal and spatial dynamics are challenging to capture in the deep sea, as few research programs can afford to survey the same area over multiple spatial and temporal scales (Woodall et al. 2018). As such, seascapes are often defined at arbitrary scales based on data availability, convenience, or a single conventional sample unit area increasing the risk of a scale mismatch (Pittman and McAlpine 2003; Lecours et al. 2015). Although conventional habitat maps are static representations, seabed structure, especially soft bottom sediment, can be relatively dynamic over temporal and spatial scales with consequences for multiscale biodiversity patterns (Zajac et al. 2013). For example, responses of macrofaunal benthos to seabed habitat heterogeneity are strongly scale-dependent. In soft-sediment environments in Monterey Canyon, faunal turnover changes were linked to scales of geographic canyon features (McClain and Barry 2010). At topographically complex seabed of the Mauritanian slope, megafaunal composition differed between broad-scale geomorphological features but exhibited limited fine-scale variability (Jones and Brewer 2012).

Landscape ecology has explored the consequences of scale more than any other ecological science and provides an evidence base and analytical tools (Jung 2016; Huais 2018) to address key questions about scale effects and guide scale selection (Wiens 1989; McGarigal et al. 2016). Exploring scale effects requires a multiscale approach, for example, using analytical windows of various dimensions. This is particularly important in the absence of any evidence to select a specific focal scale or set of analytical scales. A study in the Clarion–Clipperton zone evaluating increasing megafaunal sample area confirmed that spatial tuning of sampling units helped infer reliable ecological relationships in abyssal environments, where faunal density is typically low (Simon-Lledó et al. 2019). When employing a single scale, a minimum requirement to successfully link pattern to process is that the ecological phenomenon under consideration falls within the observational and analytical scales selected for the research (Wiens 1989; Hobbs 2003). Based on hierarchy theory, seascape approaches advocate a hierarchical scaling concept where a focal scale or ecological neighborhood (anchored in time and space to a defined phenomenon) is nested between a set of broader-scale variables and a set of finer-scale variables (Pittman and McAlpine 2003; Pittman et al. 2004). Such hierarchical approaches can provide an organizing framework to explore scale effects and help identify the most appropriate scale of analysis and response for the phenomenon under consideration (Kavanaugh et al. 2014; Porskamp et al. 2018). In map production, hierarchical approaches have been employed in several seabed habitat classification schemes such as the European Nature Information System and the Coastal and Marine Ecological Classification Standard in the United States designed to capture different levels of heterogeneity for different applications (Harris 2012). As the technological advancement of data acquisition and analysis techniques continues, sampling over multiple spatial scales and explicit consideration of scale dependencies and appropriateness of scales applied in ecological analyses remain important focal areas in seabed research (Lecours et al. 2015).

Informing ecosystem-based conservation of the deep seabed

Policy targets around sustainable use of the ocean, such as Aichi Biodiversity Target 11 and UN Sustainable Development Goal 14, advocate ecosystem approaches for biodiversity conservation (Rees et al. 2018). These recognize landscape ecology concepts related to seascape structure, connectivity, and context (e.g., habitat size and quality, habitat diversity and representation, ecological connectivity, fragmentation) as important design and evaluation criteria for area-based management tools (Crowder and Norse 2008; Pittman et al. 2021). Top-down habitat maps are the most commonly applied

strategy to identify priority areas of seabed for management planning and have become a key information source to guide and evaluate the size and shape of marine protected areas and the spatial configuration of MPA networks in the deep sea (e.g., Hogg et al. 2018). Informing the science-based design of ecologically relevant MPAs for deep-seabed environments is complicated by the limited availability of high-resolution data, and considerable knowledge gaps exist when attempting to scale up information from a few detailed study areas and when linking seascape structure to ecosystem processes. It is here that the multiscale and pattern-oriented framework developed in seascape ecology can help integrate existing data and generate new data and understanding to support operational decision making in ecosystem-based management (Young et al. 2018).

MPA design

Designing effective MPAs and networks of MPAs that address ecological coherence criteria requires spatially explicit knowledge of biodiversity distributions and the link between seabed patterning and ecological functions, including ecological connectivity (Young et al. 2018). Seascape ecology concepts and techniques have been used to inform and evaluate MPA design using pattern-derived proxies of seascape composition, configuration, connectivity and context (Huntington et al. 2010; Hilário et al. 2015; Young et al. 2018). Integrating habitat maps and spatial pattern metrics, the size, location, and shape of an MPA or network can be designed to include spatial targets for habitat representativity, replication, and redundancy, to prioritize certain seascape configurations, protect ecological corridors, or specific attributes such as to maximize or minimize edge effects (Huntington et al. 2010). Seascape ecology within a systematic conservation planning framework has considerable potential to derive spatial recommendations for MPA network design. For example, incorporating spatial information on biophysical gradients and other ecologically important features with seascape ecology principles helped design a proposal for an MPA network safeguarding biodiversity and ecosystem function in the Clarion–Clipperton Fracture Zone (Wedding et al. 2013). The connectivity of deep-sea populations is increasingly recognized as a priority research area for the establishment of such MPA networks, as disturbances to population connectivity (e.g., mining plumes) can impact their persistence as well as the effectiveness of protection measures (O'Leary and Roberts 2018; Howell et al. 2020; Danovaro et al. 2020). Since actual connectivity patterns for deep-sea species are often unavailable (Hilário et al. 2015; Baco et al. 2016), seascape ecology-based structural and potential connectivity metrics and spatial models such as IBMs and graph-theoretic approaches (Treml and Kool 2017) incorporating seascape configuration could be increasingly important for seabed connectivity analysis. For example, the implications of seascape configuration have helped to evaluate functional connectivity to promote spatial resilience, productivity, and recovery between high seas MPAs containing fragmented deep-sea populations (Kenchington et al. 2019*b*). Knowledge of such pathways may further inform the establishment of blue corridors that enhance seascape connectivity for ecologically coherent MPA networks (Hopkins et al. 2020). When focusing on ecological functions, rates of ecological processes such as carbon storage may vary as a function of biological patterning (Asplund et al. 2021). Understanding linkages between such biological seascape patterns might help understand spatial variation in carbon sequestration and storage across the deep seabed (Snelgrove et al. 2018) and help identify priority regions for conservation measures. In addition, considering the wider geographical context of MPAs and MPA networks is necessary for their ecological coherence. This includes the multiscale characteristics of surrounding environments, external drivers, and anthropogenic disturbances that may affect patterns and processes within the MPA location under consideration (Hopkins et al. 2020). Such interactions of external and internal components are typically nonlinear and can result in unexpected emergent properties that can influence the effectiveness of management approaches developed on exclusive consideration of one focal seascape (Peters et al. 2007). Buffer zones, for example, have been proposed to protect seabed MPAs from contextual disturbance effects as mining plumes (Wedding et al. 2013). Building on these principles, spatial pattern metrics may also be used to assess whether proposed or existing MPAs are meeting science-based MPA design principles. For example, a seascape ecology methodological framework successfully evaluated whether the design of the Central Coast MPA Network in California met management goals for habitat replication and representation, biological diversity, and the reduction of spill-over into adjacent fishing grounds (Young et al. 2018). In the High Seas, habitat maps combined with seascape ecology principles in systematic conservation planning have been used to assess the efficiency and representativeness of the existing MPA networks in the Northeast Atlantic, finding that the network was not the most optimal solution (Evans et al. 2015).

Monitoring seascape dynamics

As seascapes are dynamic and changes to seascape composition and configuration can affect ecological processes, an improved understanding of the drivers and the dynamic spatiotemporal character of these changes can help predict how the system will respond to stressors (Turner 2005). Spatial pattern metrics can provide a useful approach for monitoring seascape change, comparing different seascapes, or conducting impact assessments (Wedding et al. 2011). In monitoring, spatial pattern metrics have successfully been applied to assess changes in benthic community structure (Teixidó et al. 2002) and may also be applied to inform sampling design and targeted monitoring strategies, for example to target a specific functionally relevant mosaic of patch types or a specific spatial

configuration (Pittman et al. 2007). Spatial pattern metrics also have potential to quantitatively compare seascapes and evaluate how different seascape structure affects key ecological processes such as MPA rates of recovery, spatial resilience, and the provisioning of ecosystem services of interest to management. When interested in impact assessments, spatial pattern metrics may be applied to quantify and monitor the structural effects of disturbances, for example, resulting from impacts of mining and trawling (Danovaro et al. 2020), on biodiversity, ecological functions, and recovery potential. For example, Teixidó et al. (2007) applied spatial pattern metrics to quantitatively describe the patterns of recovery of Antarctic benthic communities after iceberg scouring and found that benthic cover area was the best predictor of recovery.

Summary and outlook

Environmental heterogeneity in deep-seabed environments is a recognized driver of ecological patterns and processes. By focusing on the causes, patterns, and ecological consequences of environmental heterogeneity, seascape ecology provides a theoretical framework and analytical techniques to advance the ecological study of deep-seabed heterogeneity. This review highlights with examples how the application of spatial pattern metrics at multiple scales enables a quantitative exploration of seascape heterogeneity and evaluation of its consequences on ecological patterns and processes through concepts as seascape composition, configuration, terrain structure, and connectivity, while considering the roles of context and scale. This spatially explicit, pattern-oriented approach can help address knowledge gaps around drivers and implications of spatial structure, scale dependency, and hierarchical cross-scale interactions. This may also result in insights operationally relevant to addressing real-world conservation and management challenges, such as conservation prioritization, protected area network design and monitoring of ecological change and disturbance effects. A key future focal area remains in developing appropriate metrics for measuring spatially dynamic heterogeneity in the water column (currents, nutrient coupling) influencing seabed ecology. As geospatial technology advances and data availability increases for the global deep sea, together with a demand for knowledge at scales relevant to policy and management decision making, the interest in a deep seascape ecology framework is likely to grow. If the application of landscape ecology to the deep seabed is as successful as in terrestrial and shallow-water systems in advancing our understanding of ecological patterns and processes, this field presents a highly rewarding intellectual terrain for future ecological exploration.

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Conflict of Interest

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E.2 *Mapping, quantifying and comparing seascape heterogeneity of Southwest Indian Ridge seamounts*

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RESEARCH ARTICLE

Mapping, quantifying and comparing seascape heterogeneity of Southwest Indian Ridge seamounts

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Abstract

Context Seamounts are abundant geomorphological features creating seabed spatial heterogeneity, a main driver of deep-sea biodiversity. Despite its ecological importance, substantial knowledge gaps exist on the character of seamount spatial heterogeneity.

Objectives This study aimed to map, quantify and compare seamount seascapes to test whether individual habitats and seamounts differ in geomorphological structuring, and to identify spatial pattern metrics useful to discriminate between habitats and seamounts.

Methods We mapped and classified geomorphological habitat using bathymetric data collected at five Southwest Indian Ridge seamounts. Spatial pattern metrics from landscape ecology are applied to quantify and compare seascape heterogeneity in composition and configuration represented in resulting habitat maps.

Results Whilst part of the same regional geological feature, seamounts differed in seascape composition and configuration. Five geomorphological habitat types occurred across sites, which within seamounts differed in patch area, shape and clustering, with ridge habitat most dissimilar. Across seamounts, the spatial distribution of patches differed in number, shape, habitat aggregation and intermixing, and outcomes were used to score seamounts on a gradient from low to high spatial heterogeneity.

Conclusions Although seamounts have been conceptualised as similar habitats, this study revealed quantitative differences in seascape spatial heterogeneity. As variations in relative proportion and spatial

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relationships of habitats within seamounts may influence ecological functioning, the proposed quantitative approach can generate insights into within-seamount characteristics and seamount types relevant for habitat mappers and marine managers focusing on representational ecosystem-based management of seamounts. Further research into associations of sessile and mobile seamount biodiversity with seascape composition and configuration at relevant spatial scales will help improve ecological interpretation of metrics, as will incorporating oceanographic parameters.

Keywords Habitat mapping · Geomorphology · Seamounts · Seascape ecology · Seabed · Southwest Indian Ridge

Introduction

Seamounts, typically defined as undersea mountains rising steeply from the seafloor, are some of the most prominent and widespread features of seabed topography globally (Yesson et al. 2011). They host distinct and vulnerable benthic communities forming complex biogenic habitats, and support mobile megafauna such as commercially important fish, marine mammals, and sea birds (Rogers 2018). Environmental heterogeneity, including variation in substrate type, topographic relief, and hydrodynamic exposure (McArthur et al. 2010) contribute to the ecological importance of seamounts and the high variability in faunal assemblages and distributions observed among and within individual seamounts (Rogers 2018).

Although seabed heterogeneity has long been recognised as a main driver of biodiversity in deep-sea environments (Thistle 1983), its spatial geometry is rarely quantified. Quantitative knowledge of environmental heterogeneity is key for a better understanding of seamount ecology, and could lead to insights into the potential ecological implications of spatial structuring of habitats that host and support seamount biodiversity (Clark et al. 2012; Swanborn et al. 2022). Addressing knowledge gaps around the character and consequences of benthic seascape heterogeneity is a priority because extensive physical disturbances change the spatial structure of seamount seascapes. Notably, trawling directly modifies benthic habitat mosaics with long-lasting effects due to low benthic recolonisation rates (Huvenne et al. 2016; Williams et al. 2020). A pattern-oriented approach facilitates comparisons between the structure of different seamounts, which can provide critical knowledge to classify seamount ecosystems for representational protection of their characteristics through marine protected area networks (Clark et al. 2011a).

Advances in mapping technologies and analysis techniques provide broad-scale maps from which environmental surrogates for biological communities in the deep sea can be derived (Howell et al. 2020). Measures of geomorphological structure (Wilson et al. 2007) and substrate types extracted from continuous bathymetry and backscatter acoustic maps are used as proxy for benthic communities' potential occurrence and distribution, and form input for benthic habitat maps (Brown et al. 2011). These segment and classify seascapes into areas of similar abiotic conditions that may be associated with a particular biological community. Land- and seascape ecologists have developed a wide range of analytical tools to quantify spatial heterogeneity from patch-mosaic representations as benthic habitat maps, focusing on the composition (patch types and their relative amount) and configuration (the spatial arrangement and orientation of patches) of seascapes (Wedding et al. 2011; Swanborn et al. 2022). Variations in composition and configuration influence assemblage make-up, biodiversity patterns and organism movement, and ultimately ecological processes across the seascape such as structural and functional connectivity (Pittman et al. 2021).

This study focuses on five seamounts on the Southwest Indian Ridge (SWIR). These are amongst the least scientifically studied globally, but are located in a geographic zone at high risk from fishing (Clark et al. 2011a) and have been targeted by industrial fisheries for decades (Rogers et al. 2017; Marsac et al. 2020). Data on these seamounts remain sparse, but global predictive modelling studies have linked the SWIR to potential habitat for vulnerable communities (Yesson et al. 2012) and indicate high vulnerability to human impacts (Clark and Tittensor 2010; Marsac et al. 2020). At present, knowledge gaps remain about the spatial patterns in terrain geomorphology (e.g., slope, topographic complexity) and patch-mosaic structure (i.e. seascape composition and configuration) of individual SWIR seamounts.

This study quantifies and compares spatial heterogeneity represented in geomorphological habitat maps from five SWIR seamounts varying in summit depths, shapes and sizes. The aims were to: (1) map and classify habitat types of SWIR seamounts based on geomorphological characteristics; (2) quantify and compare spatial environmental heterogeneity to test whether studied habitats and seamounts differ in geomorphological structuring; and (3) evaluate which metrics were most useful to discriminate spatial heterogeneity in composition and configuration within and between seamounts.

Methods

Data used in this study were collected during RRS *James Cook* NERC cruise JC066 in November and December 2011 (Rogers and Taylor 2012). Surveyed seamounts (Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Seamount and Atlantis Bank) vary in shape, size and summit depth (Figs. 1, 2), and are located in different water masses. More extensive morphological descriptions can be found in Muller (2017).

Study sites

Coral Seamount (41° 28′ S, 42° 53′ E) is situated east of the Discovery II Fracture Zone with a summit located at 200 m depth. The seamount is elongated from north to south over approximately 18 km. Coral is the only surveyed site located in cooler waters close to the Subantarctic Front.

Melville Bank (38° 28′ S, 42° 44′ E) is located on the eastern side of the Indomed Fracture Zone, 45 km north of the SWIR axial valley, and stretches from east to west over approximately 13.5 km. Extensive ridge features characterise the steep shallow (100 m) summit and the flanks show embayments, chutes and debris deposits.

Middle of What (MOW) Seamount (37° 59′ S, 50° 24′ E) is positioned 30 km south of the mid-axial rift valley on a rim flank uplift. It is the only surveyed location not associated with a transform fault. MOW seamount is small in height and extent, stretching over 12 km, and has a deeper summit (975 m, Fig. 2) than other surveyed sites.

Sapmer Seamount (36° 5′ S, 52° 6′ E) is located on the west flank of the Gallieni Fracture zone. The seamount is triangular-shaped and extends 17 km along the fracture zone. The summit is truncated at 250 m depth and features irregular, rough bathymetry (Fig. 2). Sapmer has volcanic ridges forming flank rift zones and slope failure processes characterise the flanks.

Atlantis Bank (32° 45′ S, 57° 16′ E) is an oceanic core complex created through fault action (Dick et al. 2019), stretching north to south 14 km along the Atlantis II Fracture Zone. The summit is flat at a depth of 700 m (Fig. 2). The western side features embayments created through mass wasting events.

Data collection

Swath bathymetry and backscatter data were acquired using a hull-mounted Kongsberg-Simrad EM120 multibeam echo sounder, operated at a frequency of 12 kHz and used with the maximum 191 beams, giving 150° coverage (Muller 2017). Any pings from beam angles greater than 120° were discounted to reduce errors. Adverse weather conditions, specifically rough sea states resulting in bubble entrainment, provided lower quality backscatter for Coral and Melville (Muller 2017, SI 1). Produced .all files incorporating navigation and sound velocity information were obtained from the British Oceanographic Data Centre (BODC) in September 2020, and Qimera 2.3.1 and FlederMaus GeocoderToolbox (FMGT) 7.9.5 (QPS) were used for further manual editing of swath bathymetry (removing spurious data points) and backscatter. Bathymetric models were gridded to a resolution of 25 m.

Analysis

The analysis consisted of three steps: (1) scale selection and terrain analysis; (2) classifying seamount seascapes in broad-scale geomorphological habitats or patch types; and (3) quantifying seascape composition and configuration represented in habitat maps. Steps 1 and 2 followed an objective unsupervised classification technique (Verfaillie et al. 2009; Ismail et al. 2015). Statistical analyses were conducted in RStudio using R v3.6.3.

The quantification of terrain morphology was conducted at two spatial resolutions: the spatial resolution of the digital bathymetric model (25 m) and a

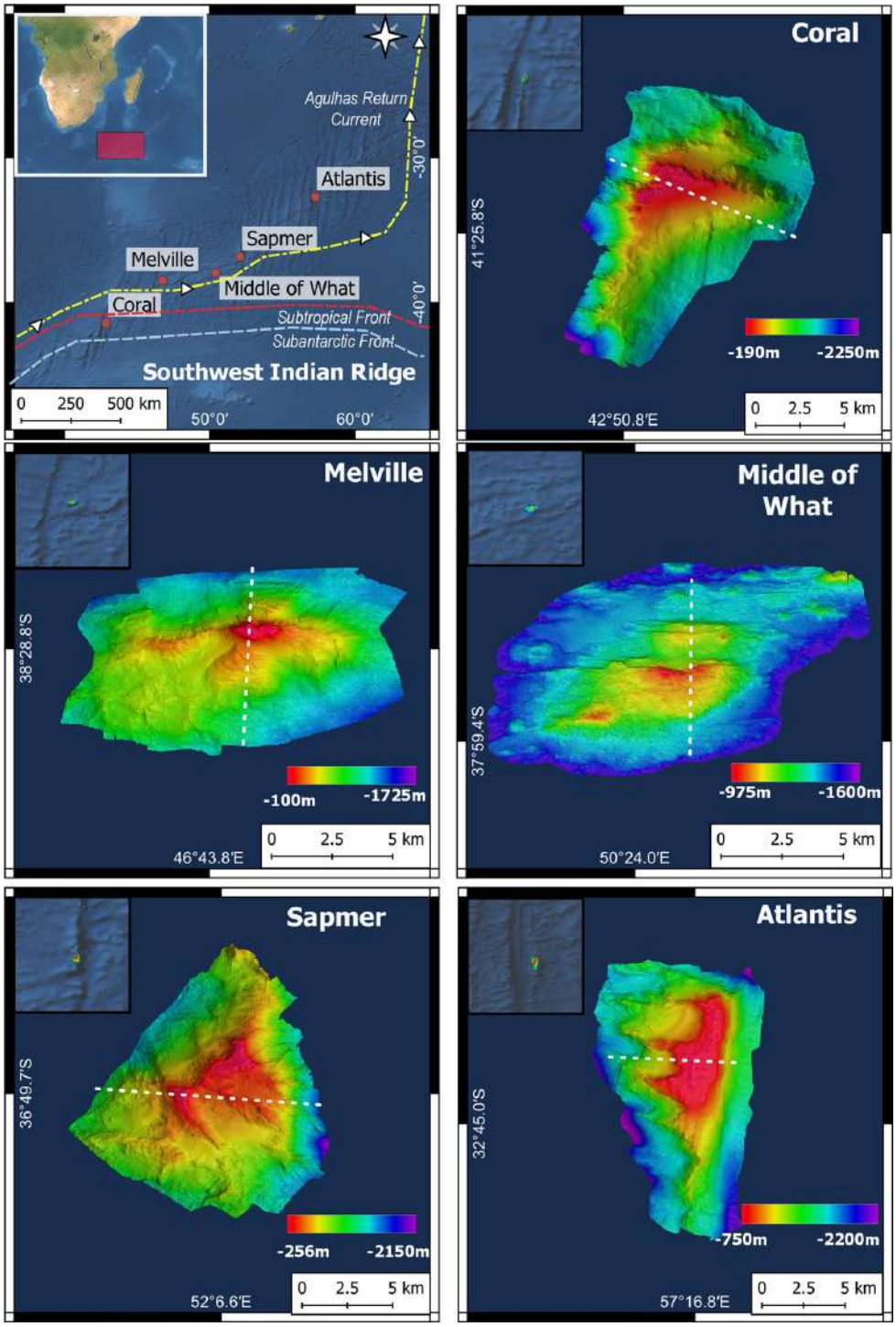


Fig. 1 Surveyed seamounts on the Southwest Indian Ridge. Individual images show seamount topography, and insets show surrounding geological context (GEBCO). White dashed lines indicate locations of cross sections in Fig. 2

broader resolution (275 m) determined using the Estimation Scale Parameter technique (Drăguţ et al. 2010), applied in R. This multiscale approach detects the scale at which an abrupt rate of change occurs in local variance (ROC-LV) and considers this the appropriate resolution to resolve potentially important landscape features. LV was calculated as the average standard deviation within a 3 × 3 moving window over 25 m spatial scale increments on bathymetry data layers created through bilinear interpolation. A

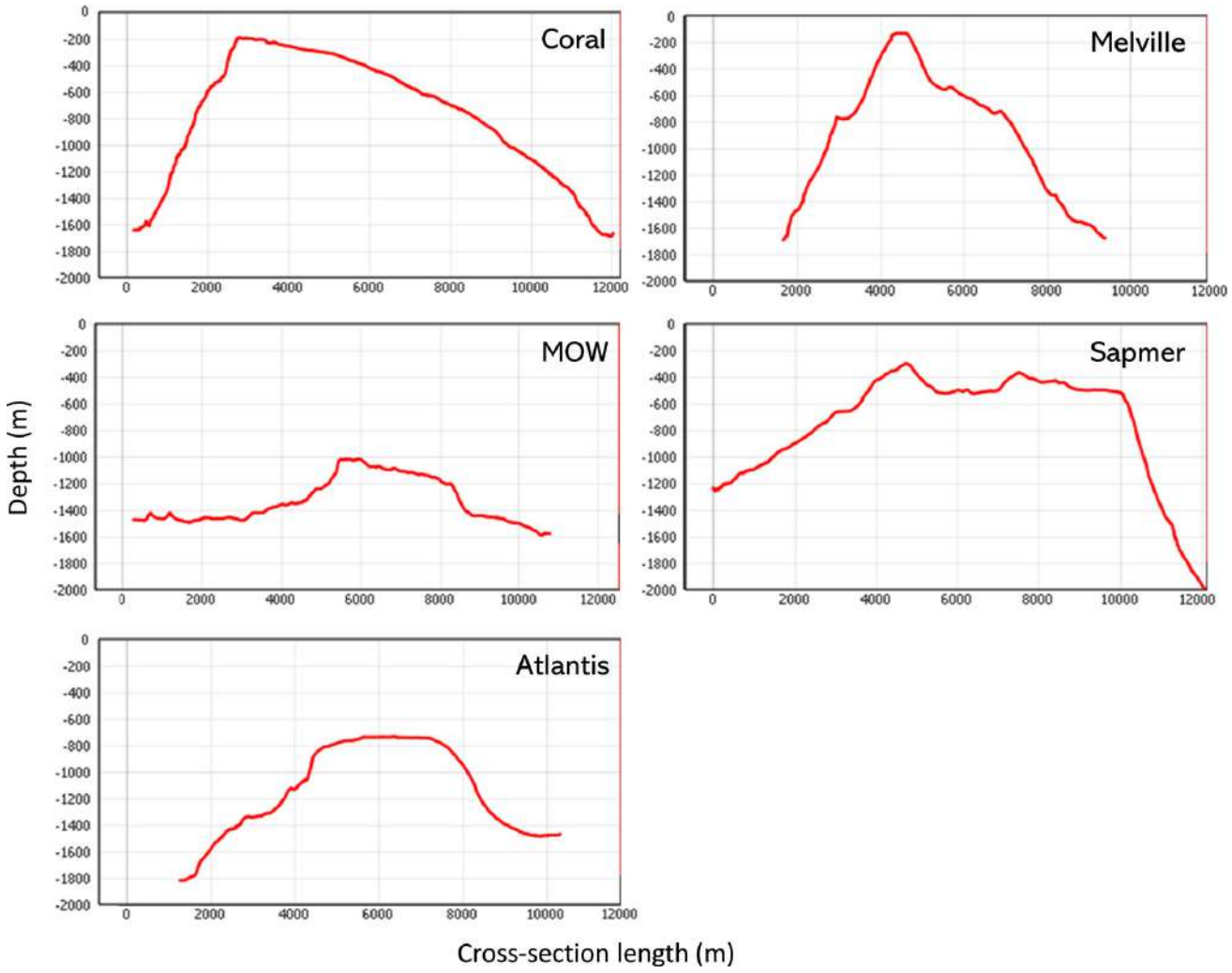


Fig. 2 Profile plots of seamounts between 0 and 2000 m depth. Locations of cross sections are indicated as white dashed lines in Fig. 1. Profiles were taken in west-north-west to east-south-east direction at Coral, west to east direction at Sapmer and Atlantis, and in north to south direction at Melville and MOW. X values represent the length of the cross-section in m (12 km)

combined ROC-LV curve (SI 2) was produced by considering its average value across scale levels to calculate the appropriate broad scale resolution across sites. A first break in the ROC-LV occurred at 275 m and was therefore taken as the resolution to calculate broad-scale predictors.

Multiple ecologically relevant variables measuring seamount geomorphology were quantified from bathymetry at the two focal spatial scales (25 m and 275 m) (Table 1). Individual seamount depth ranges were scaled and centred to correct for the absolute depth differences, thereby focusing on within-seamount geomorphological heterogeneity.

Unsupervised classification

The full dataset consisted of the values of terrain derivatives and depth at each pixel across sites, standardised to zero-mean and unit-variance to have equal weight in the analysis. The unsupervised classification consisted of two steps: Principal Component Analysis (PCA) and K-means clustering.

PCA was used to reduce data dimensionality and remove collinearity of input variables (Jolliffe and Cadima 2016). The Kaiser Harris criterion prioritised principal components (PCs) for subsequent analysis, retaining PCs with eigenvalues larger than 1. The PCs were subjected to K-means clustering (Hartigan

Table 1 Terrain metrics extracted from bathymetric data

	Terrain variable	Description	Produced in:
Terrain variables	Depth	Bathymetric surface representing depth	Qimera 2.3.1
	Slope (Horn 1981)	Rate of change of depth	R raster package
	Eastness (Horn 1981)	Direction of slope: orientation on east–west scale	R raster package, sin(aspect)
	Northness (Horn 1981)	Direction of slope: orientation on north–south scale	R raster package, cos(aspect)
	Total curvature (Zevenbergen and Thorne 1987)	Second derivative of seabed terrain, describes relative position of features	R spatialEco package, 3 × 3 neighbourhood
	Topographic Position Index (TPI) (De Reu et al. 2013)	Elevation of cells (positive or negative) compared to neighbouring cells using mean deviations	R spatialEco package, 3 × 3 neighbourhood
	Terrain Ruggedness Index (TRI) (Riley et al. 1999)	Local variation in seabed terrain around a central pixel	R spatialEco package, 3 × 3 neighbourhood
	Vector Ruggedness Measure (VRM) (Sappington et al. 2007)	Measure of ruggedness in three dimensions	R spatialEco package, 3 × 3 neighbourhood
	Slope of Slope	Rate of change of slope; measure of terrain complexity	R raster package
	Backscatter	Measure of reflectivity of seabed, corresponding to substrate type	FMGT 7.9.5

and Wong 1979), and elbow plots determined the optimum number of clusters. The bend in the plot at 5 clusters (SI 4), corresponding to a change in slope gradient, was chosen as the appropriate number of clusters. The K-means clustering algorithm, ran using 5 clusters and 500 random starting configurations, assigned each pixel of the input data a cluster membership. This final cluster solution was used to produce geomorphological habitat maps showing each pixel's cluster membership at each site. Boxplots were used to help characterise the environmental variables for each habitat.

Quantifying and comparing seascape structure

Spatial pattern metrics were applied using Fragstats v4.12 (McGarigal et al. 2012) to assess variability in seascape composition (amount and variety of patches) and configuration (spatial geometry of patches) from habitat maps (Table 2)**.** Spatial pattern metrics can be calculated at multiple levels of analysis: the individual patch, the habitat class or patch type, and the overall seascape. We selected metrics at the class and seascape level. Class-level metrics allow for comparing the composition and configuration of each identified habitat type across sites, whereas seascape-level metrics were applied to each seamount's entire habitat map to allow comparisons among locations. Class-level metrics were calculated using the mean value (sum of patch type metric values divided by the total number of patches), providing a patch-centric perspective. Seascape-level metrics were based on the area-weighted mean patch characteristics that correct for the relative size of habitat patches (McGarigal and Marks 1994).

One-way Analysis of Variance (ANOVA) with pair-wise comparisons were used to assess whether class-level characteristics differed significantly ($p < 0.05$) between habitats. Before conducting ANOVA, assumptions of normality and homogeneity of variance were checked using the Shapiro–Wilk test and Levene's test. Data were transformed using the Box-Cox family of transformations if assumptions were violated. At a seascape level, metrics with the largest variability were used to assess spatial heterogeneity between seamounts.

Table 2 Categorical spatial pattern metrics extracted from habitat maps. Metrics with separate references were developed for Fragstats with an ecological interpretation in mind, whereas metrics without references are existing concepts implemented in Fragstats

Group	Metric type	Fragstats metric and abbreviation	Description
Composition: type and abundance of patch types	*Area metrics:* basic metrics describing area composed by habitat patches	Percentage of landscape (PLAND)	Relative proportion of each patch
		Mean patch size (AREA)	Average size of individual habitat patches
	Diversity metrics: describe the compositional makeup of the landscape	Shannon diversity (SHDI)	Composite measure incorporating richness (number of different patch types) and evenness. Larger values indicate greater number of patch types and/or evenness
		Shannon evenness (SHEI)	Describes the distribution of area among patch types. Equals 1 when area is distributed evenly
Configuration: spatial arrangement of patch types	*Shape metrics*: unitless metrics describing geometric complexity of patch shapes	Shape index (SHAPE) (Patton 1975)	Perimeter area ratio corrected for patch size, where patch shape is compared to a square of the same size. Increases as patch shape becomes more complex
		Gyration (GYRATE)	Mean extent of patch. Higher indicates more elongated patch
		Contiguity index (CONTIG) (LaGro 1991)	Patch shape is assessed based on the spatial connectedness of patches. The CI increases with larger contiguous path shapes
	Isolation metrics: describe the degree of spatial isolation of patches	Euclidean Nearest Neighbour Distance (ENN)	Shortest straight-line distance between the centre of a focal patch and the centre of nearest neighbour of the same class
		ENN coefficient of variation (ENN_CV)	Measure of patch dispersion: the larger, the more irregular the spread of patches
	Subdivision metrics: describe the degree to which landscape is broken up in different patches	Number of patches (NP)	Number of different patches in landscape: the higher, the more fragmented
		Patch density (PD)	Number of patches per unit of area
		Splitting index (SPLIT) (Jaeger 2000)	Degree of subdivision; increases as the landscape is increasingly subdivided into smaller patches

Table 2 (continued)

Group	Metric type	Fragstats metric and abbreviation	Description
	Aggregation and interspersion metrics: describe the spatial distribution and intermixing of patch types	Contagion index (CONTAG) (Li and Reynolds 1993)	Measures the degree to which patch types are aggregated. Higher values indicate few large, contiguous patches with poor dispersion and interspersion, whereas lower values indicate higher dispersion and interspersion
		Clumpiness index (CLUMPY) (class only metric)	Dispersion index depicting the deviation from a random distribution. (0). Small values (-1) indicate maximal disaggregation whereas higher values (1) indicate greater clumping
		(normalised) Landscape shape index (LSI) (Patton 1975)	Ratio of total edge to area adjusted for landscape size. The larger its value, the larger internal edge and disaggregation is, whereas smaller values indicate a compact landscape. The normalised LSI is scaled between 0 and 1
		Interspersion and juxtaposition index (IJI) (McGarigal and Marks 1995)	Measures the degree to which patch types are intermixed. The higher, the more evenly interspersed patches are in a mixture of patch types

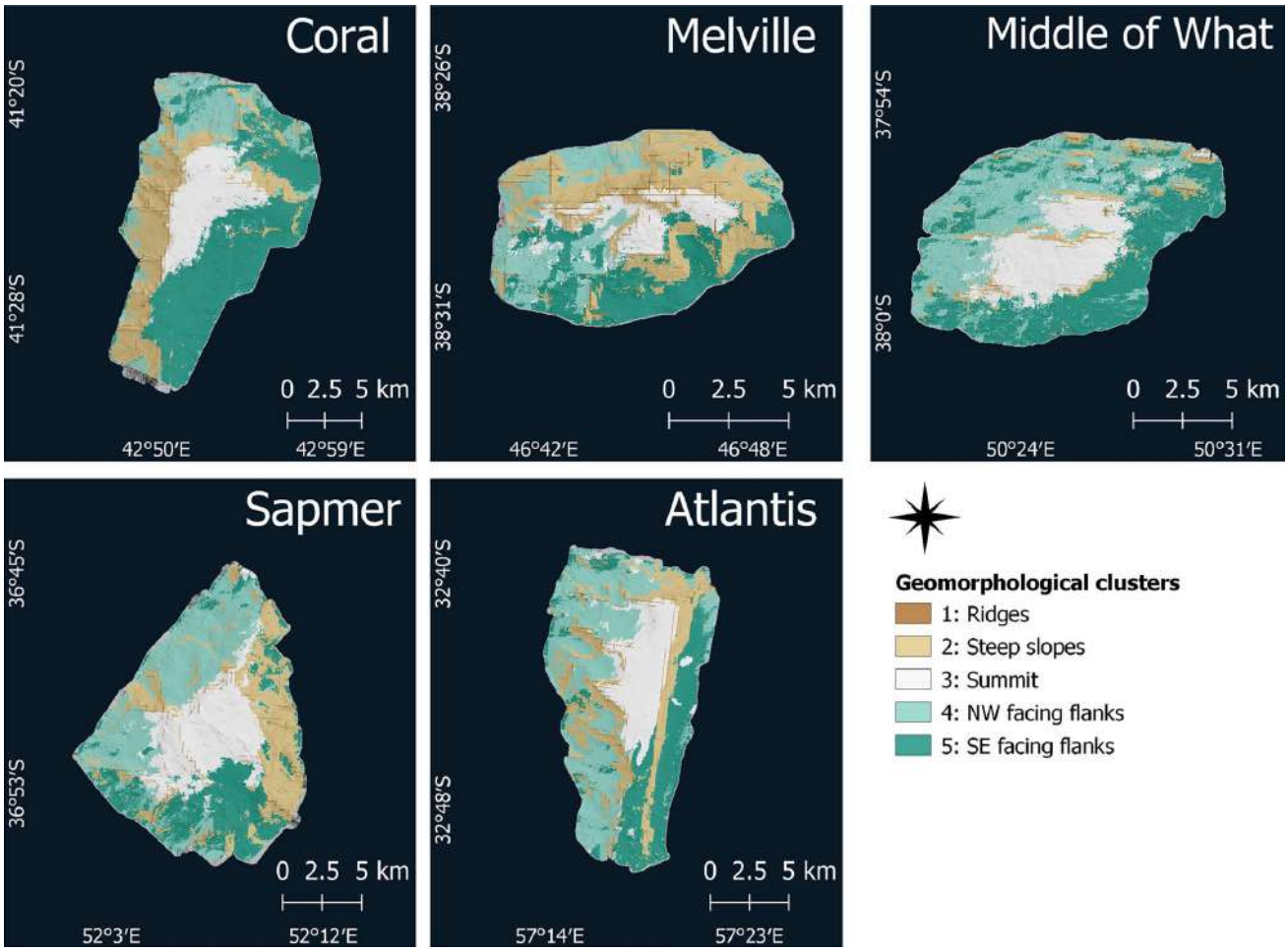


Fig. 3 Distribution of identified geomorphological clusters corresponding to habitat types at each surveyed seamount

Results

Habitat characteristics

The PCA procedure revealed nine significant (eigenvalue > 1) principal components that explained 90% of the total variance in predictor data (SI 3–1). Topographic ruggedness and slope contributed strongly to PC1, whereas PC2 consisted of depth, broad-scale curvature, and topographic position index (SI 3–2).

Habitat maps (Fig. 3) showed the distributions of five geomorphological habitat types (patch types) obtained through clustering the principal components. Maps were used in conjunction with boxplots (Fig. 4) to determine the character of identified geomorphological habitats. These were mainly distinguished by variations in slope, complexity, depth, and orientation. Habitat 1 consisted of shallower areas associated with the summit of seamounts. The terrain was flat and of low structural complexity, with local relief at individual seamounts. Habitat 2 was highly sloping (> 20°), with elevated terrain complexity. Habitat 3 and 4 were both gently sloping flank habitats (5°–20°) and distinguished by orientation (habitat 3: south/south-east/east, habitat 4: north/north-west/west). At MOW and Melville, this included far-field habitat off the main seamount structure. Habitat 5 consists of highly structurally complex and sloping terrain, linked to local highs such as crests, ridges and scarps found on the tops of the seamounts and the edges of mass wasting features.

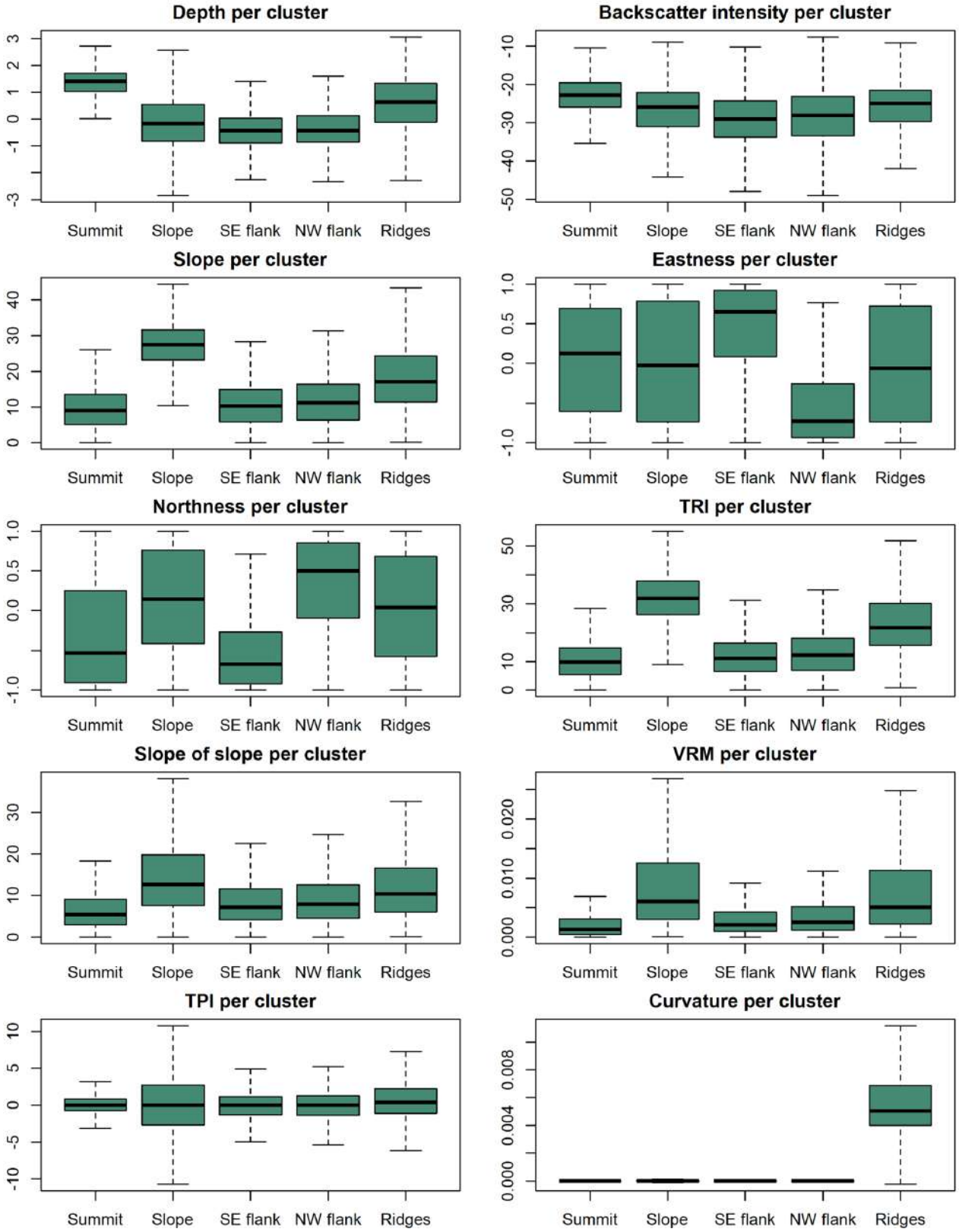


Fig. 4 Characteristics of each habitat

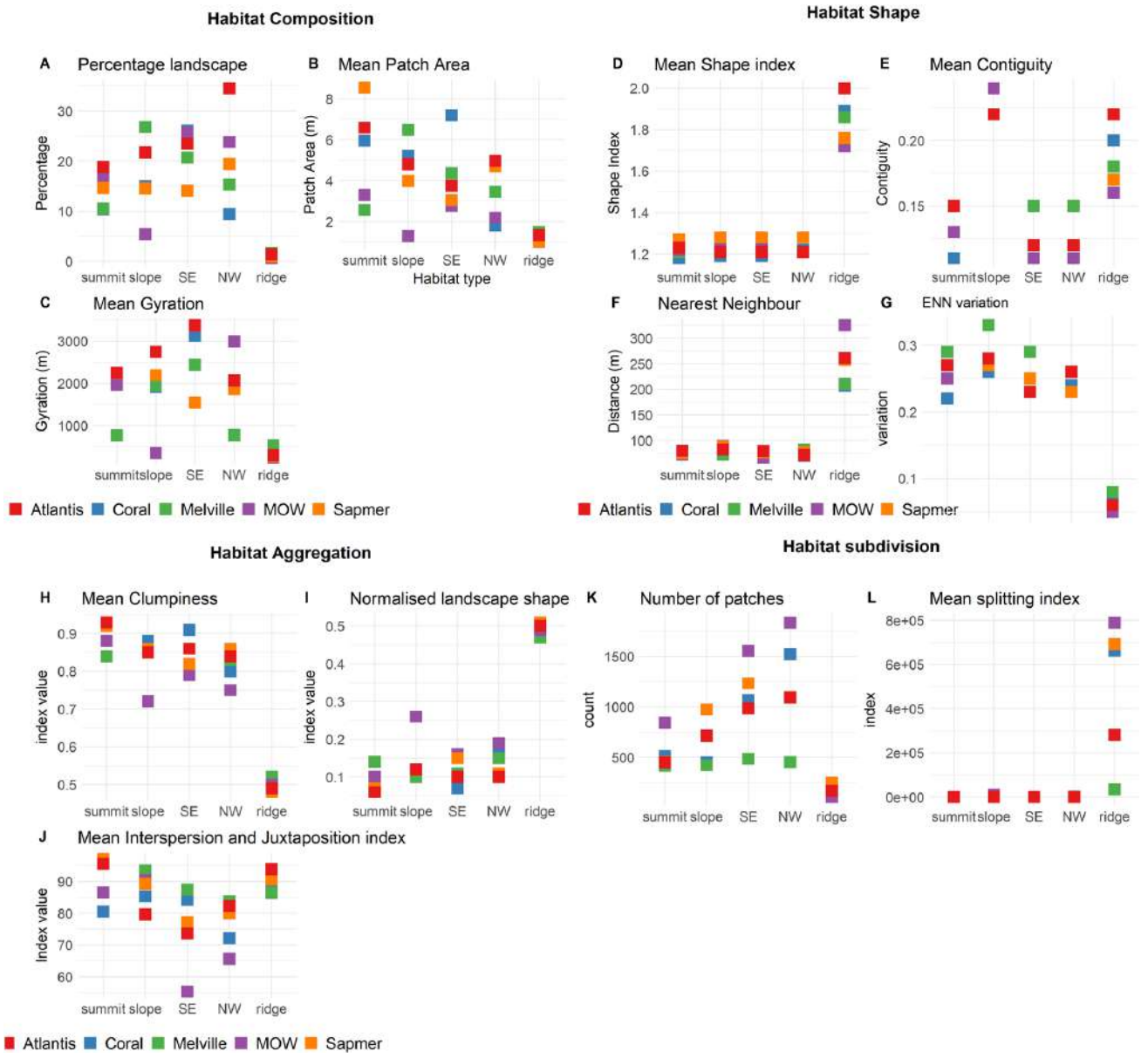


Fig. 5 Class-level metric values for each habitat type per site, arranged by metrics of habitat composition, shape, isolation, aggregation, subdivision and interspersion and juxtaposition

Structural comparison between sites

Class-level

Class level metrics (Fig. 5, SI 5–1) quantified the spatial characteristics of identified habitat types at each site, and ANOVA showed whether patch characteristics differed significantly between patch types (SI 6).

Habitat 1 Habitat 1 (summits) had larger proportional abundances, patch area and gyration at Atlantis, Sapmer and MOW (Fig. 5A, B) and occurred in contiguous and simple shapes (Fig. 5D, E). The summits significantly differed from flanks and slopes in high aggregation and interspersion, and limited subdivision (Fig. 5H, J, L, SI 6). Summit habitat at Melville was however disaggregated (Fig. 5H, I), deviating from this pattern.

Habitat 2 The relative abundance, mean size and extent of slope Habitat 2 differed across sites (Fig. 5A, B, C), with the largest proportional abundance at Mel-

ville and a limited area and extent at MOW. It significantly differed from other habitat types in a higher degree of contiguity and dispersion (Fig. 5E, G, SI 6). Subdivision, aggregation and interspersion indices also showed reduced clumping and interspersion (Fig. 5H, I, J) at MOW.

Habitat 3 South-east facing flanks formed over 20% of seamount habitat at all sites apart from Sapmer (Fig. 5A) with largest patch size and extent at Coral and Atlantis (Fig. 5B, C). Aggregation and subdivision indices indicated an aggregated occurrence pattern with high clumping (Fig. 5H, I) and low splitting, but with reduced interspersion (Fig. 5J).

Habitat 4 Composition and configuration of north-west facing flanks was not significantly different from south-east facing flanks (SI 6). The relative abundance, mean size and extent of Habitat 4 were variable per site with largest proportional abundance and patch area at Atlantis (Fig. 5A, B). Like habitat 3, distribution indices showed an aggregated occurrence pattern with least intermixing.

Habitat 5 Highly complex ridges of Habitat 5 were significantly different from all other habitat types in both composition and configuration (SI 6). It occupied a smaller percentage of landscape with a small patch size and extent (Fig. 5A–C). Patches had more complex shapes (Fig. 5D) and occurred in multiple small, disaggregated patches (Fig. 5H, I) that were spatially isolated and more dispersed (Fig. 5F, L) across sites than other habitat types.

The metrics most useful to distinguish between habitat classes (measured by the number of significant differences) were the contiguity index, the variation in nearest neighbour distance, the number of patches and the clumpiness index (SI 6).

Seascape-level

Landscape-level metrics (Fig. 6, SI 5–2) compared overall seascape structure at each seamount. Composition-wise, sites differed in area (Fig. 6C, D), but not diversity metrics (Fig. 6A, B). Configuration-wise, sites differed in seascape shape (Fig. 6E, F), subdivision (Fig. 6I–K) and seascape aggregation (Fig. 6L–N). Seascape metrics were used to rank the seamounts from lowest spatial complexity (large, contiguous patches and aggregated landscapes) to highest spatial complexity (small and complex patches, subdivided and intermixed seascapes) (Fig. 7).

At Coral, composition and shape metrics showed that mean patch size (Fig. 6C) and contiguity (Fig. 6F) were large compared to other sites. Patch shapes were relatively simple (Fig. 6E), and aggregation metrics confirmed a clumped seascape structure (Fig. 6L) with low patch density (Fig. 6J).

At Atlantis, patches exhibited relatively large spatial extent (Fig. 6D) and shape metrics suggest uniform patch characteristics. Subdivision metrics (Fig. 6J, K) indicate reduced seascape subdivision whilst aggregation and interspersion indices (Fig. 6L) suggest clumping.

Middle of What has smaller patch sizes (Fig. 6C), but with larger extent (Fig. 6D) and complex patch shapes (Fig. 6E, F). Subdivision and isolation metrics show many patches at high patch density (Fig. 6I, J) and close proximity (Fig. 6G). Aggregation indices confirmed high disaggregation (Fig. 6L, M) and limited patch intermixing (Fig. 6N). This indicates a high number of small patches in an extensive matrix of another patch type.

Patches at Sapmer were larger (Fig. 6C) and relatively contiguous. Subdivision and isolation metrics show increased isolation (Fig. 6G) and landscape splitting (Fig. 6K), which was matched by aggregation metrics confirming seascape disaggregation (Fig. 6M), reduced clumping (Fig. 6L) and, in contrast to Middle of What, intermixing of patch types (Fig. 6N).

Melville had the smallest mean patch size (Fig. 6C), and extent (Fig. 6D). Low contagion (Fig. 6L) and landscape shape (Fig. 6M) indicate limited clumping and high disaggregation, and dispersion and interspersion indices (Fig. 6N) show high intermixing of patch types.

Discussion

Geomorphological drivers of habitats

The unsupervised classification identified similar habitat types across seamounts, distinguished by variations in depth, slope, structural complexity and orientation. Depth is one of the primary determinants

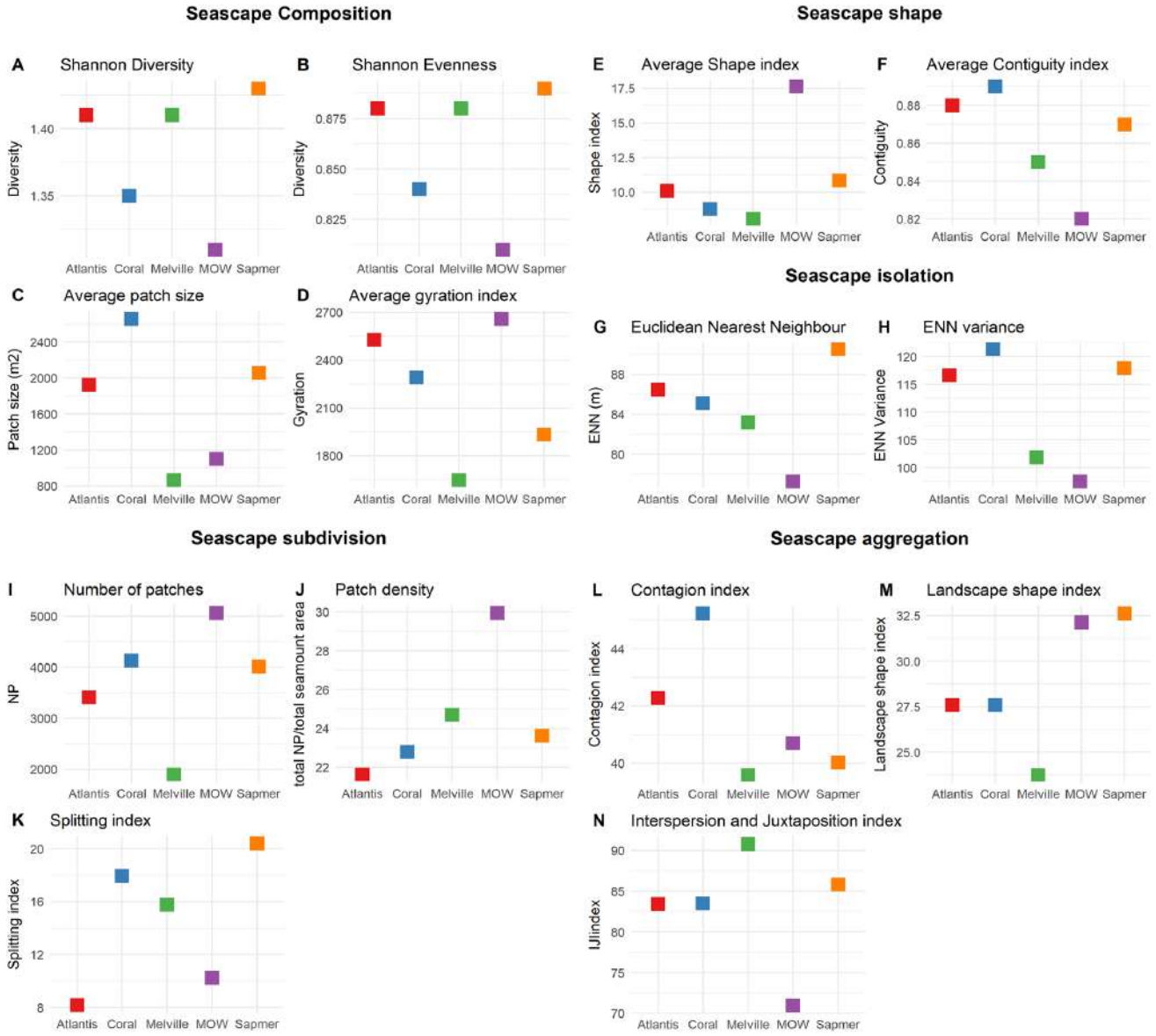


Fig. 6 Seascape-level metrics per site, arranged by metrics of seascape composition, patch shape, isolation, subdivision and aggregation

of marine biodiversity, including on seamounts, as it correlates with physical characteristics of the water column as temperature, oxygen, pressure, salinity, organic matter and light penetration. The classification established limited depth zonation within flanks and slopes. As a result of species replacement with depth these habitats likely host varying assemblages (Victorero et al. 2018), although they may be functionally similar by having comparable functional traits (de la Torriente et al. 2020). For example, steep slopes with rocky outcrops may host various cold-water coral assemblages that differ in species composition, but all function as filter feeders.

Slope, structural complexity and orientation distinguished flank habitats, summit habitat and ridges. These variables may influence exposure to local hydrodynamic regime and the deposition of sediment and organic matter (Clark et al. 2010). Steep and structurally complex features experience reduced sedimentation, accelerate hydrodynamic flow, and can result in deep ocean mixing (White et al. 2007). Nutrient availability through such current amplification can positively promote the presence of coral

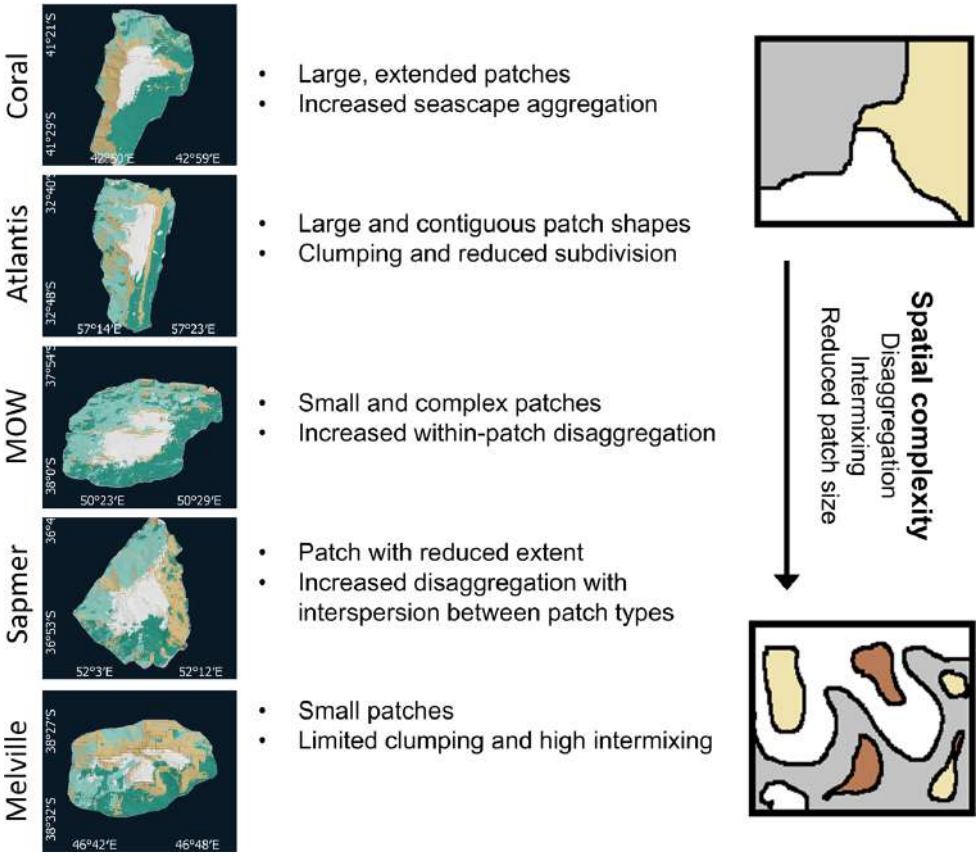


Fig. 7 Sites scored along a gradient of increasing spatial complexity. Coral and Atlantis were spatially less complex with large, contiguous patches, whereas MOW, Sapmer and Melville were more spatially complex with a larger number of patches and varying degrees of aggregation and interspersion

habitat (Quattrini et al. 2012) and seamount associated fish (Leitner et al. 2021). Orientation has been used as proxy for hydrodynamic flow and exposure to the prevailing currents. However, prevailing currents differ across surveyed seamounts because of regional processes (Pollard and Read 2017), and delineated flanks at seamounts might therefore not be directly comparable. Further research incorporating spatially explicit oceanographic parameters (Pearman et al. 2020) could help quantify environmental heterogeneity in current exposure.

Assessment of spatial heterogeneity

Habitat-level heterogeneity: differences between patches

Geomorphological characteristics of identified seamount habitats can function as predictors of benthic assemblage composition and distribution through biological associations with substratum types, structural complexity, hydrodynamic exposure and other environmental parameters (Brown et al. 2011). Metrics showed habitat types also differed in composition and configuration, with possible implications for ecology.

Flat-topped seamount summits, habitat 1, are often associated with particular substratum types, relevant for sediment-associated epifauna and infauna (Rogers 2018). The summits of Coral, Sapmer and Atlantis featured local relief as boulders, rocky outcrops, and carbonate pavement, providing attachment opportunities for sessile benthos (Rogers and Taylor 2012). This internal heterogeneity might also be ecologically relevant for certain mobile species, providing opportunities for different activities as feeding or shelter. Hydrodynamic mixing of deeper nutrient-rich water upward over the summit (White et al. 2007) may be pronounced at sites with complex summit shapes such as Melville (Read and Pollard 2017).

Highly sloping flanks of Habitat 2 are frequently associated with hard substrate for benthic settlement, and increased exposure to strong currents (Yesson et al. 2012). Video observations showed the steep western slope of Coral hosted a distinctive community of brachiopods, sponges, octocorals and black coral (Rogers and Taylor 2012). Habitat 2 was more spatially

contiguous than other habitat types. Spatial contiguity might indicate structural connectivity important for habitat-specific species (Meynecke et al. 2008). Additionally, the interspersion between other habitat types might be relevant for seamount fish and marine mammals using a wider range of environments.

Habitats 3 and 4 extended to greater depths. Backscatter data (SI 1) and limited video observations (SI 7, Rogers and Taylor 2012) indicated these flanks were covered in soft sediment patches important for benthic fauna (Durden et al. 2015) and mid- and deep water fish associated with soft substrate (Morato and Clark 2007). Flanks differed in their high spatial aggregation and large patch types, indicating extended core habitat availability but limited connection to other patch types. Combined with greater depth, these flanks are likely inhabited by specialised communities. Evidence of trawling and fishing-associated litter (Woodall et al. 2015) suggests that these large flank habitats with limited vertical relief to impede trawling (Clark et al. 2011b) are at risk of anthropogenic effects. Such disturbance can result in habitat fragmentation, impacting the highly aggregated character of these habitats.

The ridges and crests that compose Habitat 5 have high structural complexity and hard substrate, likely promoting exposure to flow. Evidence for such bathymetrically modified hydrodynamic features over ridges was observed at Coral, Melville and Sapmer (Read and Pollard 2017). Observations supported diverse biogenic habitats at ridges, with dense communities of coral, large sponges, anemones, stylasterids, black corals, octocorals and brachiopods (Rogers and Taylor 2012) which may also benefit fish assemblages (Quattrini et al. 2012; Leitner et al. 2021). The small size and fragmentation of ridge habitats show that they are typically limited and dispersed across seamount seascapes, possibly providing hotspots of highly diverse and productive benthic habitat interspersed between other habitat types.

Seascape-level heterogeneity: differences between seamounts

Composition The type and abundance of seabed habitat types influences biodiversity and ecosystem functioning (Zeppilli et al. 2016) and was measured by composition metrics. Although variable in proportional abundance, each seamount featured all five identified habitat types resulting in limited variation in diversity metrics. However, area metrics varied across sites and showed Coral, Sapmer and Atlantis featured larger patch shapes. Under theoretical ecology, larger areas are predicted to host higher species richness (Turner and Gardner 2015). Species-area relationships apply to deep-sea sessile benthic diversity across depth bands and substratum types (Foster et al. 2013), and are therefore likely applicable to seamounts too. Deep-sea mobile megafauna may be habitat specialists and predictably associated with geomorphic habitat features (Quattrini et al. 2012). The occurrence and abundance of some habitat-specific mobile megafauna may be linked to minimum area requirements and influenced by the gyration index (extent), which was particularly large for MOW, Atlantis and Coral. However, as minimum area requirements are unknown for many deep sea species environments knowledge gaps remain the transferability of such concepts.

Configuration

Patch shape Patch metrics showed that seascapes differed in patch complexity. Complex patch shapes are thought to offer limited core area and increased edge, resulting in greater exposure to external environmental conditions (Ries et al. 2017). These edge effects alter the habitat quality of patch edges in different ways, depending on biological traits and the quality differences between adjacent habitat types. Average patch shapes at Coral and Atlantis were less spatially complex, suggesting increased availability of core habitat, whereas MOW featured more complex patch shapes. Edge effects are little studied in deep-sea benthic environments, but appear relevant in the context of physical disturbances (Harris 2012). Additionally, transitions between broad-scale benthic habitat types may be less discrete than on land (Lucieer and Lucieer 2009).

Aggregation and interspersion Seascapes differed in aggregation and interspersion characteristics with possible implications for structural connectivity across the seascape. Little is known about the influence of structural connectivity on benthic and demersal fauna associated with the deep seabed, especially as many species disperse larvae through the water column (Swanborn et al. 2022). Patch aggregation is likely important for mobile habitat-specific spe-

cies with limited dispersal ranges as they facilitate movement between patches of the same type. Coral and Atlantis featured more aggregated seascape characteristics, suggesting increased habitat connectivity. Conversely, the diversity in morphological features at Middle of What resulted in higher patch disaggregation and isolation. This has been linked to reduced connectivity in terrestrial habitats, which may impact metapopulation and community dynamics of mobile species. The intermixing of patch types, such as seen at Melville and Sapmer, meanwhile, may be ecologically relevant for migratory species as large predatory fish and marine mammals that use multiple habitat types across regions and depths of the seamount (e.g. feeding and shelter) (Holland and Grubbs 2007).

Importance and methodological considerations

Relevance approach

When prioritising seamounts for protected area establishment or incorporation in marine protected area networks, an important consideration is ensuring that representative physical and biological features are included (Clark et al. 2011a, 2014), also recognised in Aichi Biodiversity Target 11 (Rees et al. 2018). Previous biogeographic classifications of seamount environments based on representation have been conducted at broad scales and did not incorporate patterns of seabed structure (Clark et al. 2011a). We showed that seamounts differ in the proportional abundance and spatial characteristics of geomorphological habitats. Seamounts differed primarily in patch size and extent (composition) and in shape, aggregation and interspersion (configuration). As these variations are likely biologically meaningful, spatial metrics could be valuable additions to broad-scale physical variables as depth and oceanographic parameters to group seamounts with similar characteristics. Based on this limited study of SWIR seamounts, the degree of aggregation and interspersion and patch shape complexity appear important descriptors of spatial variation.

This study also showed that composition and configuration can differ within individual seamounts. Different habitat features could benefit from being incorporated in the case of protection of a subset of a single seamount. For example, a zoning plan focused on protecting a seamount summit might fail to incorporate spatial representation, as ridges, flanks, and steep slopes can host different biological communities with different vulnerabilities to impacts (Bo et al. 2021) but also have different spatial characteristics.

Transferability technique

This study used a top-down classification based on terrain derivatives to identify habitat types. However, proposed approach of quantifying environmental heterogeneity using spatial pattern metrics also extends to seabed and habitat maps produced using other methods (e.g. geomorphons, semi-automated and automated approaches, Janowski et al. 2022; Summers et al. 2021) Further mapping efforts incorporating other environmental data sources could help the representation of other sources of environmental heterogeneity. For example, oceanographic variables and different water masses strongly contribute to heterogeneity, mediated by the height of the seamount, its shape, size and fine-scale topography, and the strength of the current regime (Rogers 2018). Studied seamounts were located in different water masses (Coral close to the Subantarctic Front, Melville, Middle of What and Sapmer by the Subtropical and Agulhas Fronts, and Atlantis in the Sub-Tropical Anticyclonic Gyre). Therefore ecologically important oceanographic parameters such as temperature, current velocity, dissolved oxygen and salinity likely differ between seamounts. Dynamic models incorporating spatio-temporal changes in oceanography might further refine obtained insights within seamounts (Kavanaugh et al. 2016) as oceanographic conditions at the seabed were variable over tidal cycles (Read and Pollard 2017).

Scale-dependency and ground-truthing

Here we did not consider a specific phenomenon but instead focused on quantifying and comparing broad-scale features. Although generalities will emerge, resolving the ecological implications of heterogeneity in seascape characteristics requires consideration of thematic scale. What constitutes a suitable habitat depends on the life history traits, life style (i.e. benthic, infaunal, epifaunal) and mobility of the species or process under consideration (Levin 1992). As species-environment associations were not explicitly quantified

and incorporated to inform the classification, produced maps do not intend to predict the occurrence and distribution of biological communities. However, uncovered broad-scale habitat types exhibit internal heterogeneity that may be ecologically relevant for associated species. Hierarchical classification approaches using ecological validation could help reclassify broad-scale entities into finer-scale physical habitat types and test the accuracy of identified habitat types and their spatial characteristics for particular species (Hogg et al. 2018). Considerations of appropriate thematic scale for the phenomenon under consideration will also improve the relevance and interpretation of spatial pattern metrics (Pittman et al. 2021). Seamount-associated sessile and mobile benthos have different habitat requirements than mobile megafauna as fish or mammals due to mobility ranges and life history traits.

Metric interpretation

The study also highlighted some uncertainties in the transferability of interpretations of landscape ecology metrics to deep-sea habitats. Transitions between habitat types may be less discrete (edge effects), and organisms have different dispersal strategies (water column). Also, the interpretation of metrics for sessile benthic organisms is less clear cut. Therefore, we recommend further multiscale studies testing the ecological relevance of habitat composition and configuration on sessile and mobile seamount biota, for example, generating predictor variables for explaining distribution patterns. Such knowledge would help further the conceptual importance of spatial pattern metrics from landscape ecology in heterogeneous deep-sea environments at scales appropriate for the phenomenon under consideration.

Conclusions

Using a quantitative approach combining habitat mapping and spatial pattern metrics, this study found that (1) SWIR seamounts hosted five similar geomorphological habitat types (summit, slope, south-east facing and north-west facing flanks and ridges) despite varying morphology; (2) SWIR seamounts differed in spatial composition and configuration at class and seascape level; and (3) at class-level, metrics of contiguity, isolation and clumping differentiated patch types, whereas at seascape-level patch area, intermixing and disaggregation distinguished seamounts. These variables allowed us to score seamounts on a gradient from low spatial heterogeneity (large, aggregated and isolated patches) to high spatial heterogeneity (small, disaggregated and highly interspersed patches).

Variations in spatial structure can have consequences for the biological communities, habitats and ecological processes on seamounts. The spatially-explicit approach presented here to quantify seabed heterogeneity is likely of interest to a broader community of seabed and habitat researchers, and important for considerations of representational protection of within-seamount characteristics and seamount types. To help improve ecological interpretation of metrics, we recommend further study of biodiversity associations at appropriate scales, and incorporating oceanographic parameters in mapping strategies.

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Author contribution This work forms part of the Ph.D. research of DS. DS conceptualised the study, designed the methodology, analysed the findings and drafted and revised the manuscript. ADR obtained the original funding for the fieldwork through NERC Grant NE/F005504/1 and the IUCN Seamounts Project (FFEM-SWIO-P00917). ADR, MT and LW participated in, and ADR led the research cruise during which the data for the project were collected. All authors reviewed and provided helpful comments on the manuscript.

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Data availability The bathymetry and backscatter data collected during *RRS James Cook* cruise JC066 used in this research are available from the British Oceanographic Data Centre (https://www.bodc.ac.uk/) upon request.

Declarations

Competing interests The authors declare no competing interests.

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E.3 *Seamount seascape composition and configuration shape Southwest Indian Ridge fish assemblages*

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Seamount seascape composition and configuration shape Southwest Indian Ridge fish assemblages

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ABSTRACT

Seamounts are commercially important fishing grounds. Yet, little is known about their physical characteristics as fish habitat, important for informing conservation and ecosystem-based management.

This study examines how multiscale seabed spatial heterogeneity influences commercially important fish families at three Southwest Indian Ridge seamounts (Coral Seamount, Melville Bank and Atlantis Bank). We quantified seascape heterogeneity from bathymetry and geomorphological habitat maps and identified 15 focal fish families from video data. Fish-habitat associations were examined using spatial pattern metrics that measured terrain morphology, seascape composition (variety and relative abundance of patch types) and seascape configuration (spatial arrangement of patches). Broader seascape context was characterised by geographic location and water depth. Multivariate regression trees and random forests modelled fish-habitat associations and identified the most influential explanatory variables.

Assemblage characteristics and individual families were strongly influenced by geographic location and depth, and at finer scales (500 m buffers) seascape composition and configuration helped explain fish-habitat associations. Spatially continuous summit habitat and complex shaped ridge features supported high abundance and diversity of commercial fish families. Metrics of seascape composition and configuration (i.e., habitat size, shape and structural connectivity) had higher predictive power than the terrain metrics commonly used in developing proxies for deep-water fish species and biodiversity.

These outcomes indicate that seascape metrics, commonly applied on land and in shallow marine environments, are also relevant environmental predictors of fish distributions in deep-sea environments. We highlight strong context dependency and depth-specific associations that hinder attempts to draw wider generalisations on fish-seascape linkages for seamounts.

1. Introduction

Seamounts are elevated topographic features (>100 m) on the seabed (Yesson et al., 2011. They are recognised as hotspots of benthic and pelagic diversity and support a high abundance of demersal and benthopelagic fishes compared to the surrounding environment (Serrao Santos and Morato, 2008). Fish aggregations around these elevated topographic features have also led to the establishment of deep-sea fisheries (Clark, 2009). These fisheries can have high catch-per-unit-effort ratios and large ecological impacts, exacerbated by the low growth and high mortality rates of many seamount-associated species (Pitcher et al., 2007). Despite the ecological and economic importance of seamount-associated fish, fish-habitat relationships around seamounts remain poorly understood, with only a fraction of

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total seamounts sampled (Kvile et al., 2014). Very few studies have measured multiscale heterogeneity in benthic seascape structure to examine its ecological relevance for mobile marine species. A better understanding of the linkages between seascape characteristics and fish assemblages may have significant implications for ecology, ecosystem-based fisheries management and biodiversity conservation (Leitner et al., 2021; Santos et al., 2021).

Environmental gradients and patchiness in abiotic and biotic conditions are characteristic of seamounts. Varying topography, substrate types, the overlying hydrodynamic regime and benthic cover create gradients and patchiness in a range of habitat types, influencing biological diversity at the seafloor (Goode et al., 2021; McClain and Schlacher, 2015). Heterogeneity can be represented and quantified in terms of patch mosaic composition (the variety and relative abundance of habitat types), spatial configuration (the arrangement of patches), and terrain surface morphology (Pittman et al., 2021; Wedding et al., 2011). Quantitative seascape ecology studies of the effect of seascape composition, configuration and terrain structure have yielded important insights into the fish communities of shallow marine systems including, for example, those exploring the importance of the type, size and shape of habitat features (Boström et al., 2011), their spatial configuration (Meynecke et al., 2008), and those including understanding the influence of spatial scale and context (Forman, 1995; Pittman et al., 2004).

Studies measuring deep-water fish-habitat associations, including at seamounts, have predominantly focused on depth and substrate characteristics, revealing that deep-water fishes use a range of habitat types over different scales (Auster et al., 2005; Quattrini et al., 2012). Fish may use biogenic features for shelter or food sources (Rogers et al., 2007), feeding aggregations are seen on larger features such as summits and crests (Leitner et al., 2021; Morato and Clark, 2007) and soft-sediment areas of low complexity can host significantly different assemblages compared to complex habitat types (Devine et al., 2020; Ross et al., 2015). The diversity of broad-scale habitat or patch types and their abundance (seascape composition) is therefore ecologically relevant for mobile species across depths (Anderson et al., 2009; Borland et al., 2021). Additionally, the spatial characteristics of the local and surrounding seabed environment (seascape configuration) appear to influence the distribution and abundance patterns of deep-water demersal fishes (Anderson et al., 2009).

Despite an increasing interest in studying the influence of habitat characteristics on deep-water fish (e.g. Leitner et al., 2021), key knowledge gaps remain on the importance of the spatial patterns of habitat patches, terrains and the surrounding seascape for seamount-associated fish, as well as on the transferability of theoretical frameworks developed on land to the deep sea (Swanborn et al., 2022b). Yet, similar questions, concepts and quantitative techniques for measuring heterogeneity in terrestrial landscapes and in shallow waters may provide insights into the importance of environmental heterogeneity for demersal fish associated with seamounts. Improved data quality and availability of *in-situ* biological survey data collected using remotely operated vehicles (ROVs), combined with high-resolution bathymetry and habitat mapping, provide unprecedented opportunities to explore the ecological relevance of benthic seascape patterns on biological assemblages (Swanborn et al., 2022b).

The Southwest Indian Ridge (SWIR) seamounts remain poorly studied, yet have been subject to intense deep-sea fishing activity over the past 40 years (Rogers et al., 2017; Woodall et al., 2015). Some seamount aggregating species such as orange roughy (*Hoplostethus atlanticus)*, pelagic armourhead (Pentacerotidae), oreos (Oreosomatidae) and alfonsino (*Beryx* sp.*)* are highly valued by commercial fisheries, leading to intense exploitation (Clark, 2009; Clark et al., 2007; Rogers, 2017). Although SWIR seamounts are known aggregation spots for commercially important species, little is known about the physical habitat characteristics that support them (Rogers, 2013). Knowledge on the potential function of seascape spatial patterns as a proxy for predicting fish assemblages can inform management, for example, by identifying and characterising priority areas for conservation (Clark et al., 2012; Moore et al., 2016).

This study aims to identify commercially important demersal fish families at three SWIR seamounts and examine the ecological importance of seabed environmental heterogeneity at multiple spatial scales for these families by employing the theoretical framework of seascape ecology. To identify ecologically important seascape features, we assess 1) whether seamount assemblages differ between depth zones and seamounts; and whether seascape composition and configuration are key drivers of 2) assemblage characteristics (abundance, richness and diversity) and 3) individual fish families.

2. Methods

2.1. Study locations

Data used in this study were collected during the 2011 JC066 cruise aboard RRS *James Cook* (Rogers and Taylor, 2012). The considered seamounts, Coral Seamount (Fig. 1b), Melville Bank (Fig. 1c), and Atlantis Bank (Fig. 1d), are located along the ultra-slow spreading SWIR and characterised by varying morphologies and summit depths. They are positioned within different regional oceanographic conditions created by the Agulhas Return Current, the Sub-Tropical Front and the Sub-Antarctic Front, which influence the biodiversity these seamounts host (Fig. 1a) (Pollard and Read, 2017; Rogers et al., 2017).

2.2. ROV surveys

To survey demersal fish populations, upslope video transects were conducted with the ROV Kiel 6000 (Fig. 1). The ROV, where possible, was run at 1m above the seabed at approximately 0.2 kts and carried a CTD for *in-situ* oceanographic measurements. While the sampled depth ranges overlap across the three features, due to weather conditions and seamount morphology, sampling effort and average depth surveyed differed per site (Table 1). Dives at Melville Bank were conducted at the shallowest depths, Coral Seamount contained the majority of dives in the bathyal zone (>1000 m) and Atlantis Bank contained predominantly dives in the twilight zone (200–1000 m).

2.3. Biological data

Continuous annotation of underwater video data collected by the ROV was conducted with QuickTime Viewer (Apple Inc.), where a screenshot was taken for every fish sighting during the dive (Malpas, 2017). Every sighting was then identified to the lowest taxonomic level possible (Malpas, 2017) using a combination of reference books (Gon and Heemstra, 1990; Whitehead, 1985) and the online database FishBase (Froese and Pauly, 2020). A full list of species observed at the three seamounts, including those not analysed in this study, can be found in Appendix A. Substratum type (bedrock, boulders, cobbles, gravel, mud, rubble, cold-water coral reef, mesophotic coral reef) was also recorded from these screenshots according to the majority rule (the dominant cover determines the substratum type). When no substrate type was visible in the screenshot (e.g. as a result of camera orientation or bad visibility) substrate type was recorded as 'NA'. All sightings were linked to ROV track metadata using timestamps containing position (latitude, longitude, depth) and oceanographic data (temperature, salinity, pressure).

The continuous ROV dives were divided into separate transects to derive comparable sampling units. The appropriate transect length was determined by iteratively testing different transect lengths in steps of 25 m (the resolution of bathymetry) between 50 and 700 m. The transect length maximising both the number of samples (transects) and the number of individuals incorporated in the analysis was 250 m (Figure B1 in Appendix B). Identified transects were spaced a minimum of 100 m apart to create individual sampling units. Transects with fewer than

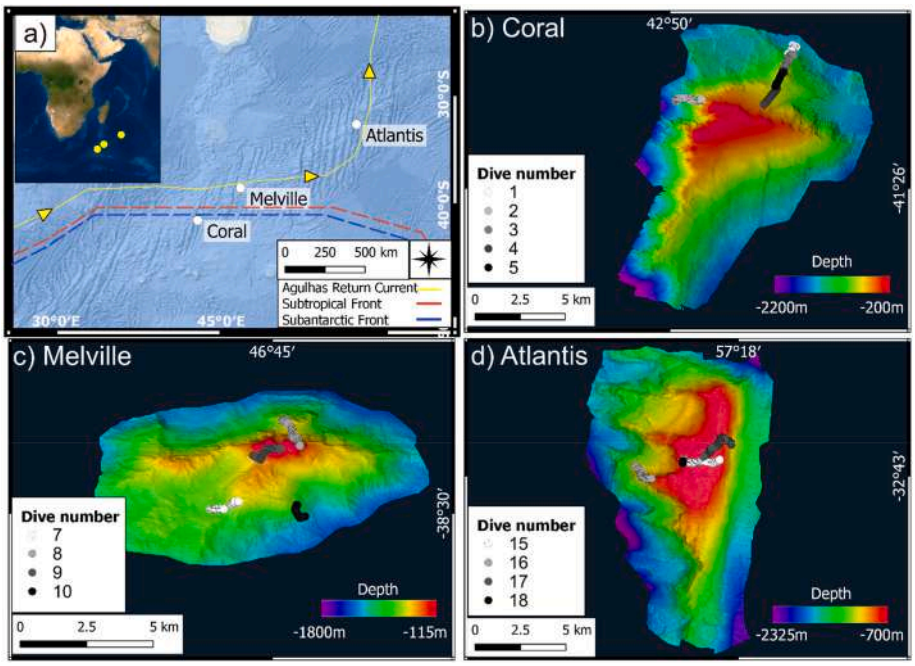


Fig. 1. Surveyed SWIR seamounts described in Rogers and Taylor (2012). Panel a indicates the location of the three surveyed seamounts and dominant influences on local oceanography. Subsequent panels show multibeam bathymetry and location of ROV dives) at Coral (b), Melville (c) and Atlantis (d) (note different horizontal and vertical scales). Colour bars indicate seamount depth. Dives differed in depth range surveyed, dive time and distance covered. Dive 6 was a sample collection dive and therefore not included. Dive 11–14 were conducted at locations not considered in this study.

Table 1
Characteristics of conducted ROV dives (Rogers and Taylor, 2012). Dives were semi-randomly selected to cover different geomorphological features of each seamount and differed in depth range surveyed, dive time and distance covered.

Site	ROV Dive no.	Date	Depth range (m)	Dive time (min)	Distance (m)
Coral Seamount	1	12/11/2011	1400–1090	506	1533
	2	13/11/2011	1493–622	507	3518
	3	14/11/2011	1065–681	597	1870
	4	16/11/2011	745–510	270	2305
	5	20/11/2011	738–731	316	1025
Melville Bank	7	23/11/2011	900–671	442	1827
	8	24/11/2011	675–150	505	1946
	9	25/11/2011	380–125	414	1638
	10	26/11/2011	1295–970	334	972
Atlantis Bank	15	09/12/2011	720–748	640	2639
	16	10/12/2011	1100–825	385	1428
	17	13/12/2011	1000–720	519	3353
	18	14/12/2011	740–730	98	130
Total				**6649**	**29672**

three fish present were removed to enable subsequent statistical analysis. The final number of transects analysed in this study was 55 (17 at Coral; 19 at Melville; 19 at Atlantis). Fish from 20 commercially important families (Rogers et al., 2009, 2017) were recorded per transect (Table 2), and all analyses were conducted at family level. Families with fewer than three observations were removed from the analysis.

Observations were standardised by transect duration (obs/duration in hours) before calculating total abundance, richness (number of families), and Shannon diversity index (using the total number of individuals and the number of individuals of each family) per transect. This was deemed appropriate because ROV speed differed across transects due to current-driven variations, and this study focuses on highly mobile species.

2.4. Environmental data

For each transect, we identified descriptive parameters (site, depth, substratum type and distance to nearest ridge feature, oceanographic parameters) and quantified variables describing terrain structure and seascape composition and configuration in three different sizes of area (250m, 500m, 1000m) surrounding transects, referred to as 'buffer zone' in the remainder of the paper (Table 3).

Terrain structure was extracted from bathymetric data at a raster cell resolution of 25 m × 25 m (Rogers and Taylor, 2012). Orientation, slope, terrain complexity (VRM, TRI) and curvature (including TPI) (Wilson et al., 2007) were quantified within a 3 × 3 moving window using R packages raster (Hijmans, 2017) and spatialEco (Evans, 2017) and the average value for each terrain derivative was recorded per transect (Table 3). Benthic seascape composition and configuration were measured using unsupervised seabed habitat maps (Swanborn et al., 2022a) at a raster cell resolution of 25 m × 25 m. To produce these maps, geomorphological habitat types were determined through K-means classification in R v3.6.3. Depth-normalised terrain characteristics from 5 SWIR seamounts, Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Bank and Atlantis Bank (using relative depth, slope, curvature, terrain complexity and aspect) formed the input for the analysis. Five habitat types were identified and mapped out: seamount summit, ridges, slopes, NW flanks and SE flanks. Habitat maps were used to identify seascape composition (proportion of habitat types, their size, abundance, richness and diversity) and configuration (spatial configuration of habitat types, full list of metrics in Table 3). These were quantified in multi-scale sample units extending 250 m, 500 m and 1000 m around each transect with Fragstats 4.2 (McGarigal et al., 2012) (Fig. 2). Fragstats is a spatial analysis program. It uses the areal extent and spatial distribution of patches (in this case, habitat types) from categorical maps of landscapes (in this case, seascapes) to obtain measures of landscape structure (Table 3).

Collinearity between derived variables was analysed using the

Table 2
Commercially important fish families observed at Coral, Melville and Atlantis, including species-level observations common name and ROV dives in which species from this family were observed. Families in bold font represent the 15 families that were retained in the analysis.

Family	Species	Common name	ROV Dive no.
Berycidae (alfonsinos)	*Beryx* sp., *Beryx splendens*	Splendid alfonsino	4,5,7,15,17,18
	Centroberyx druzhinini		
Carangidae (amberjacks)	*Seriola lalandi*	Yellowtail amberjack	9
Centrolophidae (medusafishes)	*Centrolophus niger*	Black ruff	7, 10, 15, 17, 18
	Hyperoglyphe antarctica	Bluenose warehou	
Cyttidae (dories)	*Cyttus traversi*	King dory	8, 15
Etmopteridae (lantern shark)	*Etmopterus* sp,	Lantern shark	3, 4, 7, 8, 10, 15,
	Etmopterus spinax	Velvet belly lanternshark	17
Gempylidae (escolars)	*Promethichthys prometheus*	Roudi escolar	1, 7, 17
Hexanchidae (cow shark)	*Hexanchus griseus*	Bluntnosed sixgill shark	2, 17
Latridae (trumpeter)	*Nemadactylus monodactylus*	St Paul's fingerfin	9, 17
Moridae (morid cod)	*Guttigadus kongi*	Austral cod	1, 2, 3, 4, 5, 7, 8,
	Mora moro	Common mora	9, 10, 15, 16, 17
	Guttigadus sp.	Morid cod	
	Laemonema compressicauda	Morid cod	
	Lepidion sp.		
	Physiculus sp.	Morid cod	
	Tripterophycis sp.	Morid cod	
		Morid cod	
Nototeniidae (Antarctic cod)	*Dissotichus eleginoides*	Patagonian toothfish	1
Odontaspididae (sand shark)	*Odontaspis ferox*	Smalltooth sand tiger	9
Ophidiidae (cusk eel)	*Ophidiidae* sp	Cusk eel	5
Oreosomatidae (oreos)	*Allocyttus niger*	Black oreo	1, 10, 15, 16, 17
	Neocyttus rhomboidalis	Spiky oreo	
	Oreosoma atlanticum		
	Pseudocyttus maculatus		
		Ox-eyed oreo	
		Smooth oreo	
Pentacerotidae (armourheads)	*Pentaceros richardsoni*	Pelagic armourhead	15, 16, 17, 18
Polyprionidae (wreckfish)	*Polyprion americanus*	Atlantic wreckfish	2, 7, 8, 9, 15, 17
	Polyprion oxygeneios	Hapuku wreckfish	
Scorpaenidae (scorpionfish)	*Scorpaenidae* sp.	Scorpionfish	7, 8, 9, 10, 15, 17
	Scorpaena sp.		
Scyliorhinidae (catshark)	*Apisturus* sp.	Ghost catsharks	10, 17
	Bythaelurus naylori	Dusky snout catshark	
Sebastidae (rockfish)	*Heliconus dactylopterus*	Blackbelly rosefish	2, 4, 7, 8, 9, 15, 17
	Trachyscorpia sp.		
	Sebastes norvegicus	Rockfish	
		Rosefish	
Squalidae (dogfish shark)	*Squalus mitsukurii*	Shortspine spurdog	15, 17, 18
Trachichthyidae (slimehead)	*Hoplostethus atlanticus*	Orange roughy	2, 4, 10, 15, 16, 17, 18

Spearman correlation index. Of variable pairs with a correlation >0.7, one variable was removed based on the variables' ease of interpretation. Measures of seascape composition and configuration were highly collinear between buffer sizes. The strength of associations between biological metrics and the metrics extracted from the different buffer sizes were identified to identify the appropriate scale of analysis. Metrics extracted from 500 m buffers exhibited stronger correlation with family abundance, and were retained. A total of 18 variables describing environmental structure was used for analysis (Table 3).

2.5. Analysis

All modelling and analysis was conducted in R version 4.0.3.

2.5.1. Assemblage composition with site and depth

To assess whether seamount assemblages differ between depth zones and seamount (geographic location), a PERMANOVA (Permutational Multivariate Analysis of Variance) was conducted on the Bray-Curtis dissimilarity matrix over 999 permutations. The time-corrected abundance data matrix was fourth-root transformed before analysis to reduce the effect of dominant outliers such as abundant schooling fish (i.e. Polyprionidae, Oreosomatidae). Pairwise comparisons were performed post-hoc using the R package *pairwiseAdonis* (Martinez Arbizu, 2020). Additionally, indicator species analysis (Cáceres and Legendre, 2009) determined whether families exhibited significant associations with sites or depth classes. A nMDS (non-metric multidimensional scaling) plot was used to visualise compositional similarities in fish assemblages between transects.

2.5.2. Assemblage-level responses to seascape heterogeneity

Regression trees and random forests (Breiman, 2001) tested associations of assemblage characteristics (abundance, richness and diversity) with predictor variables. These approaches were chosen for their ability to explore potentially complex non-linear fish-seascape associations, including interactions between predictors (Knudby et al., 2010).

Binary regression trees, implemented through R package rpart v4.1.16 (Therneau and Atkinson, 2019) visualised the main structure of regression relationships. Trees for abundance, richness and diversity were fitted using 10-fold cross-validation. Tree size (number of splits) was controlled by optimising the complexity parameter (cp) value to maximise cross-validation accuracy with high R squared values.

Random forests, implemented using R package RandomForestSRC v3.1.1 (Ishwaran and Kogalur, 2021), assessed the importance and influence of predictor variables on assemblage characteristics. Models were implemented by bootstrapping without replacement and tuned to minimise the cross-validated prediction error (out-of-bag or OOB error). Tuning involved setting the optimum number of variables selected as candidates for splitting node (mtry) and the minimum size of the terminal node. The OOB data was used for a performance assessment using variance explained (R Squared) and the error rate. Confidence intervals evaluating the change in Mean Squared Error over 200 random permutations assessed variable importance, with significance tested at the alpha = 0.05 level (Breiman, 2001). Partial dependence plots subsequently showed the response of assemblage characteristics to significant predictor variables. Variable interactions were tested using maximal subtree analysis (Ishwaran and Kogalur, 2007).

2.5.3. Fish family responses to heterogeneity

As individual fish families may have specific habitat associations (Moore et al., 2016), multivariate alternatives of regression trees and random forests were applied to test whether families are associated with particular combinations of environmental variables.

Multivariate regression trees (MRTs) (De'ath, 2002), implemented using R package mvpart v1.6–2 (De'ath, 2014), explored, explained and predicted relationships between multispecies data and environmental characteristics. They were constructed using 10-fold cross-validation, and the optimum tree size was chosen using the lowest value for the relative cross-validated error.

Multivariate random forests (MRFs) (Segal and Xiao, 2011), implemented using the package RandomForestSRC v3.1.1 (Ishwaran and

Table 3
Measures of environmental structure explored for use in models, including abbreviated names used in the analysis where applicable. The 18 variables retained are indicated.

Type	Metric	Description	Scales	Retained?
Descriptive	Site	Seamount name		**Yes**
	Depth	Continuous (m)	Transect	**Yes**
	Distance to ridge feature (RidgeDist)	The closer to a ridge the higher the likelihood of high productivity	average	**Yes**
Oceanography	Temperature	Temperature (°C)	Transect	No, highly collinear with depth
	Salinity	Salinity (g/kg)	average	No, highly collinear with site
	Pressure	Pressure (bar)		No, highly collinear with depth
Terrain structure	Slope	Slope angle (degrees)	Transect	**Yes**
	Slope of slope	The change of the slope gradient, acts as measure of terrain variability	average	No, highly collinear with VRM
	Vector Ruggedness Measure (VRM)	Measure of terrain complexity		**Yes**
	Terrain Ruggedness Index (TRI)	Local variation in seabed terrain, associated with changes in habitat complexity		No, highly collinear with slope and proportion of sloping habitat
	Curvature	The orientation and relative elevation of the surface		No, highly collinear with TPI
	Topographic Position Index (TPI)	Measure of curvature – indicates relative elevation		**Yes**
	Aspect (eastness and northness)	Measures of terrain orientation		**Yes**
Composition	Substratum type	Cold water coral, mesophotic reef, coral rubble, gravel, boulders, cobbles, bedrock and sediment veneer, mud	Transect average	**Yes**
	Proportion of habitat - summit (Summit_prop), slope, SE flanks (SE_prop), NW flanks (NW_prop), ridges (Ridge_prop)	Proportion of each patch type in surrounding environment	Buffers (250m, 500m, 1000m)	**Yes x4 (500m buffer) –** apart from proportion of sloping habitat (highly collinear with slope and TRI)
	Mean patch area (PatchArea)	Average size of patches in surrounding environment		**Yes (500m buffer)**
	Patch abundance and richness	Measures of the number of patches present and the number of different types		No, highly collinear with Shannon evenness and diversity, patch area, landscape shape index, interspersion and juxtaposition and division index
	Shannon Diversity in seascape structure	Diversity metrics incorporating the number of patch types and their relative abundance		No, highly collinear with Shannon evenness, landscape shape index and division index
	Shannon Evenness in seascape structure			No, highly collinear with Shannon diversity, landscape shape index and division index
Configuration	Contagion	Extent to which patch types are aggregated or clumped. Higher values indicate increased aggregation.	Buffers (250m, 500m, 1000m)	**Yes (500m buffer)**
	Mean Shape Index (PatchShape)	Quantifies average shape of patches by using a ratio of patch perimeter to patch surface area: higher values indicate more complex shapes.		**Yes (500m buffer)**
	Mean Euclidean Nearest Neighbour (ENN)	Measure of average proximity between patches. Lower values indicate more connected seascape.		**Yes (500m buffer)**
	Interspersion and Juxtaposition index (Interspersion)	Measure of intermixing.		**Yes (500m buffer)**
	Landscape shape index (LandscapeShape)	Measure of patch disaggregation. Higher values indicate more disaggregation and internal edge.		**Yes (500m buffer)**
	Division index (Division)	Measure of splitting. Higher values indicate a more subdivided landscape.		No, highly collinear with landscape shape index, Shannon diversity and evenness and patch richness

Kogalur, 2021), extended MRTs with subsampling techniques from random forests. MRFs were constructed using bootstrapping without replacement and tuned the number of candidates for splitting node (mtry) and the minimum size of the terminal node. Model performance was assessed using the mean OOB prediction error (standardised mean squared error) and average OOB variance. Ten model resamples repeating this process were created to assess precision.

For each family, the model resample with the lowest mean squared error was selected to calculate confidence intervals of variable importance over 200 random permutations, similar to traditional random forests. The five most important variables were recorded for each family and partial dependence plots showed fish family responses to these variables. The number of times each variable occurred as one of the five primary drivers was recorded to identify the relative importance of terrain structure, composition, and configuration metrics. Finally, variable interactions were tested using maximal subtree analysis (Ishwaran and Kogalur, 2007).

3. Results

3.1. Assemblage composition with site and depth

The final modelling dataset contained 1053 fish observations including at least 47 unique taxa from 15 commercially important families. The most abundant families were the Polyprionidae (wreckfish, $n = 270$), followed by the Moridae (morid cod, $n = 216$), Oreosomatidae (oreos, $n = 133$), Latridae (trumpeteers, $n = 124$), Squalidae (dogfish sharks, $n = 110$), and Pentacerotidae (armourheads, $n = 81$). The most widespread families, measured as the number of transects in which they were present, were the Moridae ($n = 44$), Scorpaenidae (scorpionfishes, $n = 20$), Sebastidae (rockfishes, $n = 18$) and Oreosomatidae ($n = 16$).

The PERMANOVA revealed significant differences in fish assemblages between depth zones (photic, twilight and bathyal), sites, and interaction effects between site and depth, with the majority of variance attributed to site effects (40%) (Table C1 in Appendix C). Pairwise comparisons (Table C2) showed that assemblages differed significantly

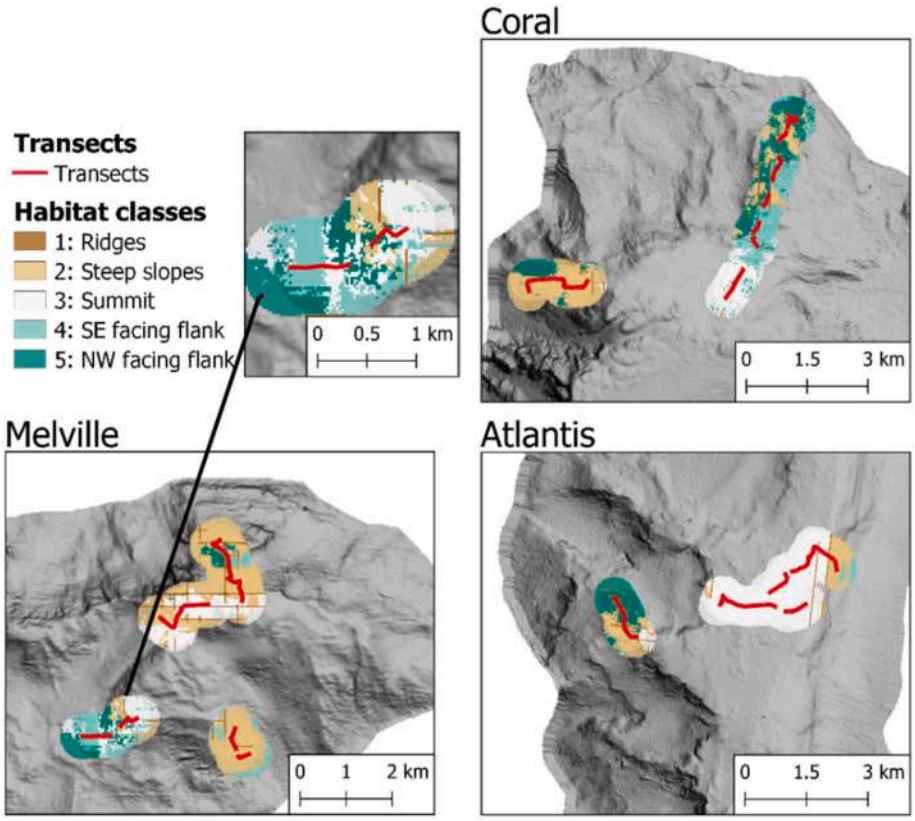


Fig. 2. Spatial visualisation of environmental data extraction. 500m buffers were created around the 250m transects (red lines) and used to quantify seascape composition and configuration using the occurrence and spatial distribution of habitat types (top left). Remaining panels show 500m habitat types in buffers and 250m transects plotted on hillshade maps of Coral, Melville and Atlantis.

between all sites ($p < 0.05$), with Coral Seamount most different from other sites. Further, pairwise comparisons between depth zones (Table C3) showed that assemblages differed significantly ($p < 0.05$) between the photic and bathyal zone and between the photic and twilight zone (defined in Table 4), but not between the twilight and bathyal zone. As photic transects were only found at Melville, the PERMANOVA was also run excluding these four transects. Site and depth class were still significant influences on assemblage characteristics (Table C4), but the importance of site effects was decreased (28.8%).

Indicator species showed that the majority of families (10 out of 15) in the modelling dataset were significantly ($p < 0.05$) associated with a site and/or a depth zone (Table 4). These findings were apparent in the nMDS (Fig. 3), which showed that fish abundance was driven by site and depth as well as family associations.

Table 4
Associations of family occurrence with site and depth zone. Bold font and star indicate significant association.

Site	Families
Coral	**Moridae***
Melville	**Carangidae***, Etmopteridae, **Latridae***, **Polyprionidae***, **Scorpaenidae***, **Sebastidae***
Atlantis	**Berycidae***, Centrolophidae, Gempylidae, Hexanchidae, **Oreosomatidae***, **Pentacerotidae***, **Squalidae***, Trachichthyidae
Depth Range	**Families**
Photic zone (0–200m)	**Carangidae***, **Latridae***, **Polyprionidae***, **Scorpaenidae***, **Sebastidae***
Twilight zone (200m–1000m)	Berycidae, Centrolophidae, Gempylidae, Pentacerotidae, Scorpaenidae, Sebastidae, Squalidae
Bathyal zone (>1000m)	Etmopteridae, Hexanchidae, Moridae, Oreosomatidae, **Trachichthyidae***

3.2. Assemblage-level responses to heterogeneity

Regression trees (Fig. 4) explained 87% of variation in abundance and 77% of variation for both richness and diversity, but had cross-validated errors of over 50%. This indicates high explanatory power, but limited predictive power. The influence of the main splitting parameters was identified by random forests (Fig. 5), which explained 40.73% of variation in abundance, 42.3% of variation in richness and 52.75% of variation in diversity, but equally had higher error rates. The main driving variables of assemblage characteristics are depth, site, the proportion of summit and the proportion of ridge in surrounding buffers, patch shape and landscape shape.

Fish abundance (Fig. 4a) is strongly dependent on depth, with shallower areas (>-400m) characterised by highest abundances. In the twilight and bathyal zones, more complex patch shapes support higher abundance. For simpler patch shapes substrate characteristics are important, and patches with gravel, rubble or cold-water coral host higher abundances than patches with boulders and sediment veneer or mud. Random Forests (Fig. 5a and b) confirmed a strong dependency of abundance on depth and a positive association with complex patch shapes and disaggregated seascapes. Some evidence of variable interactions were observed (Fig. D1 in Appendix D) between Depth and Patch Shape.

Family richness (Fig. 4b) is driven by site, and transects surveyed at Coral host lower richness than Atlantis and Melville. At Atlantis and Melville, areas with higher proportions of summit, high structural complexity and complex patch shape support highest richness. For transects with a lower proportion of summit, the proportion of ridge habitat in surrounding buffers positively influences richness. Random Forests (Fig. 5c and d) confirmed lowest richness at Coral, and positive associations with an increased proportion of summit and ridge habitat

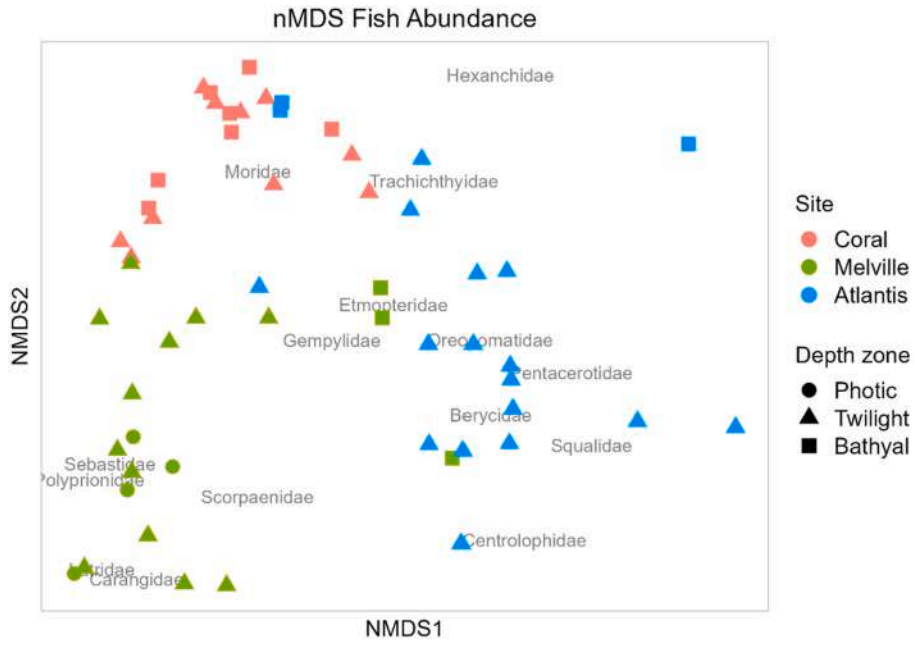


Fig. 3. nMDS (stress = 0.08) conducted on standardised fish abundance data confirming site- and depth driven separation of assemblages. Symbol colours denote the seamount, and symbol shapes denote the depth zone (photic: <200m, twilight: 200m–1000m, bathyal: >1000m).

and complex patch shapes. They additionally showed an effect of depth, with higher family richness in shallower transects. There was no evidence of interactions between variables included in the model (Fig. D2), apart from weak ties between Site and the proportion of summit.

Shannon diversity in assemblage structure (Fig. 4c) is equally site-dependent, with higher diversity in the transects surveyed at Atlantis and Melville than at Coral. At Atlantis and Melville, more aggregated landscapes with high structural complexity host highest diversity, followed by more diverse landscapes with small patch areas. At Coral, diversity is higher in more sloping areas. Random forests (Fig. 5e and f) revealed an additional effect of the proportion of summit habitat and a positive, but not significant, association with the proportion of ridge habitat. However, resampled variable importance confidence intervals revealed that only site, proportion of summit and landscape shape were significant ($p < 0.05$) drivers. No variable interactions were observed (Fig. D3), apart from weak ties between site and landscape shape (simpler landscape shapes at Atlantis).

3.3. Family-specific responses to heterogeneity

Multivariate regression trees on untransformed family abundance data (Fig. 6) explained 74% of variation, but, like the single regression trees, had low predictive power. Primary splits (depth, patch shape, proportion of ridge and summit and site) matched those obtained for the univariate variables.

Multivariate random forests modelled the effects of measures of heterogeneity on individual families. Across families, MRFs explained an average 34% of variance, but had low predictive power indicating results do not readily generalise. Model performance (Fig. 7) varied between families and depth zones. Overall, model performance was best (higher variance explained, lower error rate) for photic and twilight families occurring in higher abundances (Latridae, Carangidae, Polyprionidae, Pentacerotidae, Squalidae). Most families for which reduced model performance was observed (Etmopteridae, Centrolophidae, Hexanchidae, Gempylidae) were bathyal and had a lower number of observations in the modelling dataset. As fish occurrence is heavily influenced by heterogeneity of oceanographic parameters in addition to terrain parameters, family models with variance explained of over 30% were deemed acceptable (Berycidae, Carangidae, Latridae, Moridae, Oreosomatidae, Pentacerotidae, Polyprionidae, Sebastidae, Squalidae) following similar values in shallow reef studies (Costa et al., 2014; Pittman et al., 2009).

Associations with seascape composition, configuration and terrain structure were assessed per depth class. Families associated with the photic zone were Carangidae, Latridae, Polyprionidae, Scorpaenidae and Sebastidae (example of plots are given for Sebastidae in Fig. 8). Variable importance plots for these families (Fig. E1 in Appendix E) revealed a combined effect of site and depth. Melville Bank was the only site where the photic zone was surveyed as it was the shallowest seamount summit. Habitat composition also affected abundance, with the proportion of slope and ridge habitat positively driving abundance of Polyprionidae, Carangidae and Scorpaenidae, but Sebastidae showed negative associations with ridge habitat. Some families also showed weak associations with the proportion of summit (Latridae, Polyprionidae) or SE flanks (Latridae, Carangidae). For Latridae, substratum type (mesophotic reef) was important. Of the configuration metrics, patch shape was important for Sebastidae (Fig. 8), indicating a role of spatially simple patch types.

Families associated with the twilight zone were Pentacerotidae, Squalidae, Berycidae, Gempylidae and Centrolophidae (Fig. E2). Most of these families were affiliated with transects at Atlantis Bank and showed a positive association with the summit. There was a strong role for configuration metrics with abundance increasing with increased patch area (Pentacerotidae, Centrolophidae), complex patch shapes (Pentacerotidae, Squalidae) and aggregated landscape characteristics (Pentacerotidae, Squalidae, Berycidae, Centrolophidae). Some families (Pentacerotidae, Gempylidae) also appeared dependent on complex patch shapes.

Families associated with the bathyal zone were Etmopteridae, Hexanchidae, Moridae, Oreosomatidae and Trachichthyidae (Fig. E3). Only models for Oreosomatidae and Moridae had reliable performance. Across families there was a dependence on site and depth, with families at Atlantis Bank (Trachichthyidae, Oreosomatidae, Hexanchidae) associated with increased proportions of ridge habitat and/or reduced summit proportion. Effects of configuration metrics were mixed, but small patch areas (Oreosomatidae, Etmopteridae), increased contagion (Moridae, Etmopteridae), landscape clumping (Moridae, Hexanchidae) and complex patch shapes (Hexanchidae, Oreosomatidae) were

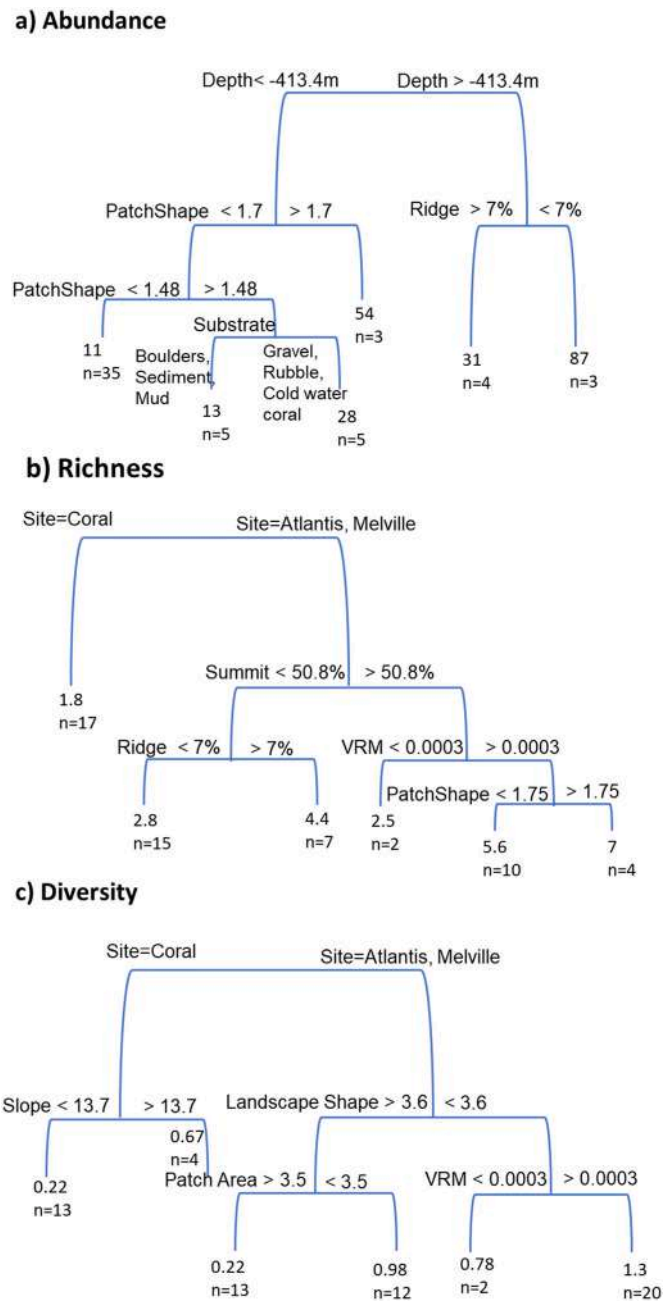


Fig. 4. Regression trees for a) Abundance, b) Richness and c) Shannon Diversity. Splits indicate important breaks in variable values, whereas end nodes indicate average abundance, richness and diversity values and the number of observations in that split.

influential.

Summing the times that each variable appeared in the main five predictor variables of each family (Fig. 9), key variables were site and depth, followed by configuration measures (landscape shape, patch shape and patch area), and composition measures (proportion of summit, ridge and flank). The importance of terrain metrics (VRM, TPI, northness and eastness) was reduced. Limited predictor interactions were found in the maximal subtree analysis (Fig. E4) for Depth, Landscape Shape and Patch Shape.

4. Discussion

4.1. Fish assemblages with site and depth

Assemblage composition differed between the transects surveyed on each seamount. Fish abundance, diversity and richness was lowest in the transects surveyed at Coral Seamount and few of the families found at other sites were found here. Melville Bank was the shallowest seamount surveyed, with a summit hosting a high abundance of predatory fish including amberjacks, wreck fishes and trumpeteers. The summit of Atlantis Bank was deepest, but transects surveyed at this site hosted high fish diversity, richness and abundance, including oreos, pelagic armourhead and orange roughy.

These differences in faunal composition may be explained by the highly dynamic and variable oceanographic conditions created by the Agulhas Return Current, the Subtropical Front, and the Sub-Antarctic Front (Rogers et al., 2017) influencing the geographic distribution of surveyed fish families. Oceanographic conditions including parameters like temperature, salinity, oxygen, water mass, and current strength at Coral Seamount, which are highly correlated with depth, were strongly different from the other sites. It was the only seamount located in cooler, more saline and oxygenated sub-Antarctic waters close to the Sub-Antarctic Front and south of the Agulhas Return Current and Subtropical Front (Pollard and Read, 2017). Melville Bank is located just north of the Subtropical front and Agulhas Return Current, and therefore exposed to dynamic conditions that can vary between Subtropical and Sub-Antarctic. Additionally, its summit extends into the photic zone and provides unusual and isolated shallow water habitat compared to the surrounding ocean, explaining the occurrence of mesophotic coral ecosystems and the high abundance of fish also found in shallow reef environments. Atlantis is located further northeast in the Subtropical Anticyclonic gyre. It experiences weak eddy currents and semi-diurnal upwelling creating varying productivity patterns (Read and Pollard, 2017) likely important for the high diversity of found fish communities. It is notable that observations on the biodiversity of pelagic species across the studied section of the Southwest Indian Ridge showed similar division of communities attributed to water mass variation from bacterioplankton to micronekton (midwater shrimps and gnathophausiids, cephalopods) and nekton (Djurhuus et al., 2017; Laptikhovsky et al., 2017; Letessier et al., 2017). Knowing that survey depth is a major driver of deep-sea biodiversity and correlated with parameters as temperature and pressure (Table 3), the varying average site survey depth may further emphasise some of the broad-scale biological patterns found.

4.2. Responses to seascape heterogeneity

Fish-habitat associations were mainly driven by depth and site, but seascape metrics (composition and configuration) proved useful to describe habitat associations at studied locations in more detail.

4.2.1. Seascape composition

Seascape composition, the type and abundance of different broad-scale bathymetric habitat types (summit, ridge, slope, flanks), strongly influenced fish assemblages.

The proportion of summit habitat was particularly important. At Coral Seamount and Melville Bank, higher proportions of summit habitat were associated with higher richness and diversity - noting the summit of Coral Seamount was not as extensively surveyed as those of Melville and Atlantis- and at Atlantis the abundance of multiple families (Berycidae, Pentacerotidae, Squalidae) was dependent on the proportion of summit habitat. In other geographic areas, seamount summits have also been shown to host higher biological abundance, richness and diversity than other parts of the seamounts (González-Irusta et al., 2021; Porteiro et al., 2013). Processes operating on seamount summits are different from those on flanks, for example the exposure to topographically induced physical circulation. Although no evidence of Taylor

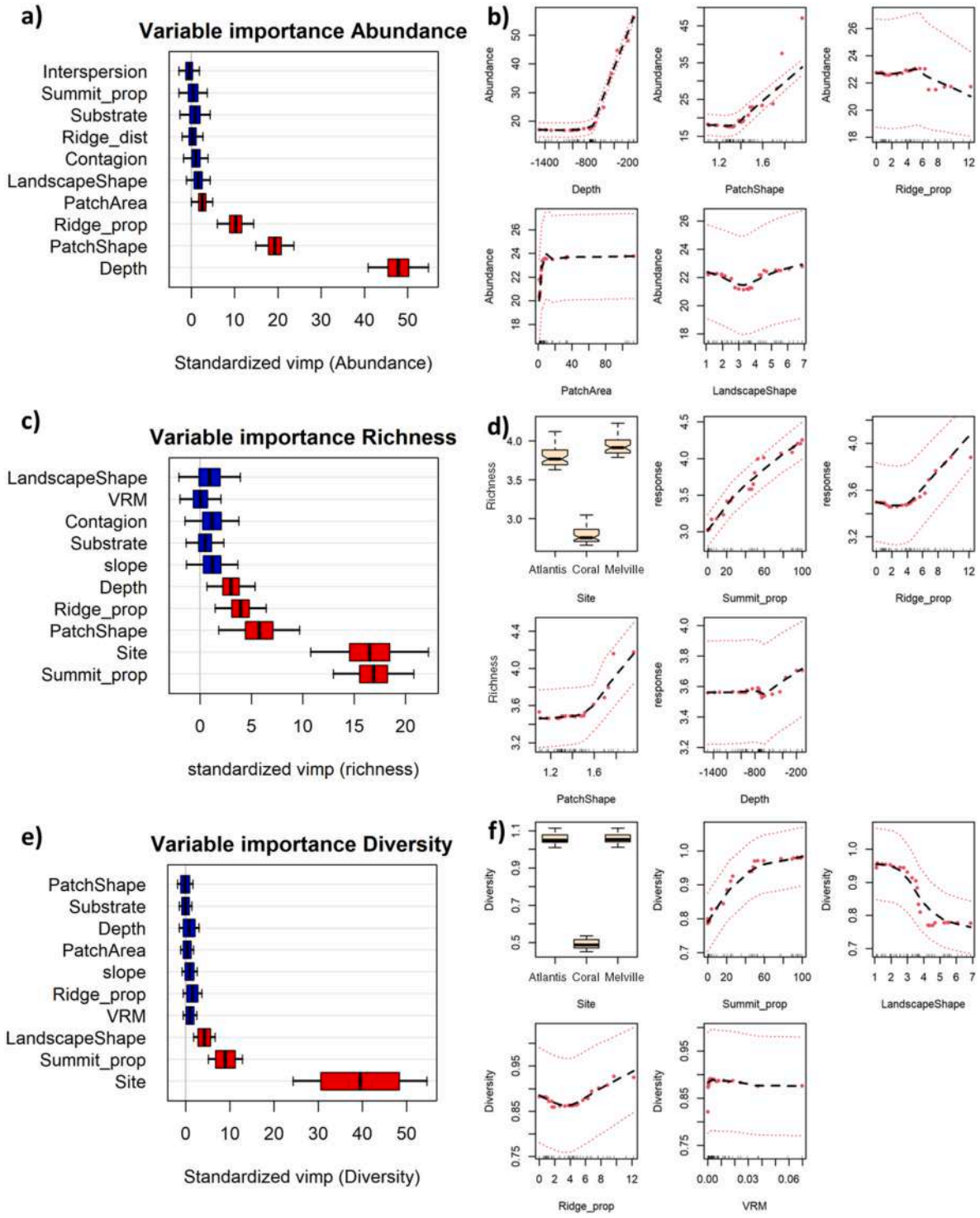


Fig. 5. Importance and effect of seascape heterogeneity on abundance (a,b), richness (c,d) and diversity (e,f). Left-hand panels indicate variable importance (vimp) of the 10 main variables obtained through resampling, with red colours indicating a significant ($p < 0.05$) effect. Right-hand plots show partial responses to the main 5 (including significant) parameters, where black dashed lines and red points indicate the partial values, and the dashed red lines indicate an error bar of two standard errors.

columns was found at these seamounts in a 2009 study, internal tide formation, tidal driven up and down welling and mixing was observed around seamount crests (Read and Pollard, 2017). These may influence nutrient and prey availability (Clark et al., 2011; White et al., 2007) potentially resulting in community differences as we found here.

The second important habitat type was the proportion of ridge features. Local topographic elevations such as ridges and crests have been demonstrated to positively benefit fish biodiversity (Leitner et al., 2021), but our results only partly matched those observations. A higher proportion of ridge features was positively correlated with richness, but did not significantly affect abundance or diversity. However, ridges were a key determinant of the abundance of several individual families (Carangidae, Oreosomatidae, Scorpaenidae, Trachichthyidae). The partial effect of ridge habitat may be related to the fact that, as for

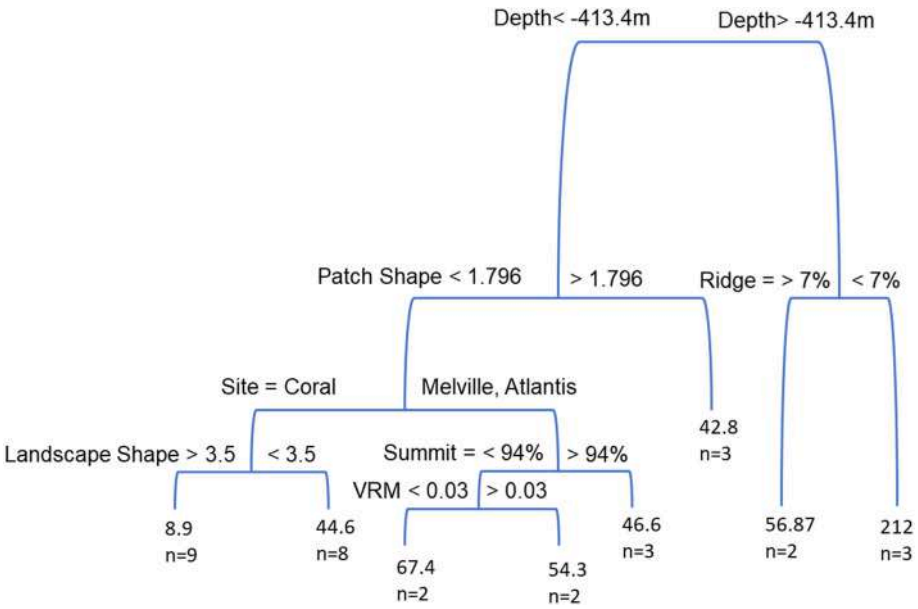


Fig. 6. Multivariate regression tree of fish family abundance. Splits indicate important breaks in variable values. End nodes indicate average abundance and the number of observations in that grouping.

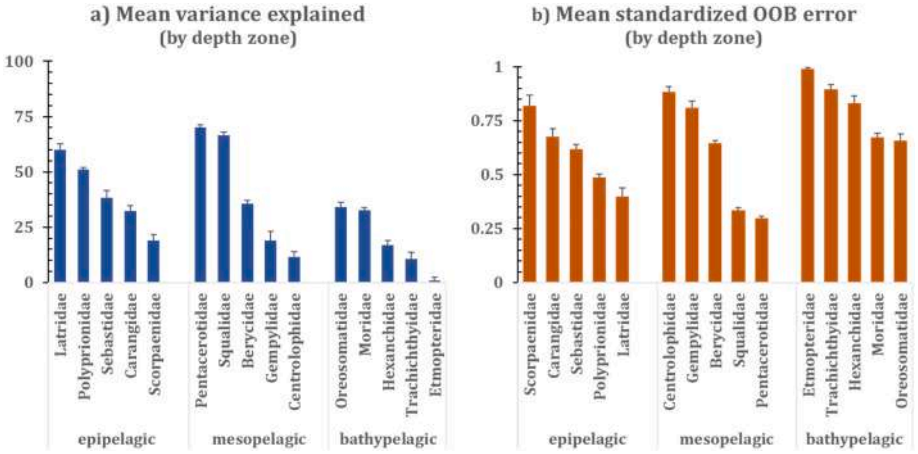


Fig. 7. Model performance of multivariate random forests measured by variance explained (a) and standardized out-of-bag error (b). Error bars represent standard deviations over 10 model resamples.

summit habitat, ridges did not receive equal survey effort across sites. Additionally, the broad spatial resolution at which habitat maps were produced may not be appropriate for all surveyed assemblages (Kendall et al., 2011).

Despite the importance of steeply sloping habitat for biodiversity through possible current amplification and effects on prey availability (see for example Leitner et al., 2021, in a shallower survey at 300–400m), the analysis did not reveal a clear effect of these features on demersal fish assemblages, apart from at Coral where steeper slope gradients were correlated with higher diversity. Similar to slope, the proportion of flank habitat did not appear to influence assemblage characteristics. When flank habitat occurred in the top five driving variables for families (Gempylidae, Carangidae, Latridae, Hexanchidae), abundance had a negative association with the proportion of flank habitat suggesting that flanks hosted lower abundances of fish. However, flank habitat was only extensively surveyed at Coral, where overall fish abundance, diversity and richness were lower than at the other sites. A more extensive survey of flank habitat at Melville Bank or Atlantis Bank might support a more reliable assessment of the importance of flank habitat. Assemblages on flanks may show high specificity and diversity because of taxa only found at deeper depths (González-Irusta et al., 2021). Flank habitats are also more prone to trawling than other parts of the seamounts, which might further influence fish assemblages. Video observations confirmed historical or ongoing fishing activity at all three seamounts (Rogers and Taylor, 2012; Woodall et al., 2015).

It is important to recognise that habitat maps were created without ground-truthing benthic assemblage occurrence or substratum types and instead are based on geomorphological characteristics of the terrain. Although substratum types were captured as separate predictive variables in the analyses, incorporating ground-truthing in the production of habitat maps may provide a more detailed view on the effect of habitat composition and configuration on demersal fish.

4.2.2. *Seascape configuration*

Incorporating configuration metrics helped assess the effects of patch area, patch shape and seascape aggregation on fish assemblages and individual families.

Larger patch sizes were expected to positively influence abundance. On land, many species have minimum patch size requirements (Godron, 1981), which also appear important for demersal fish species (Anderson

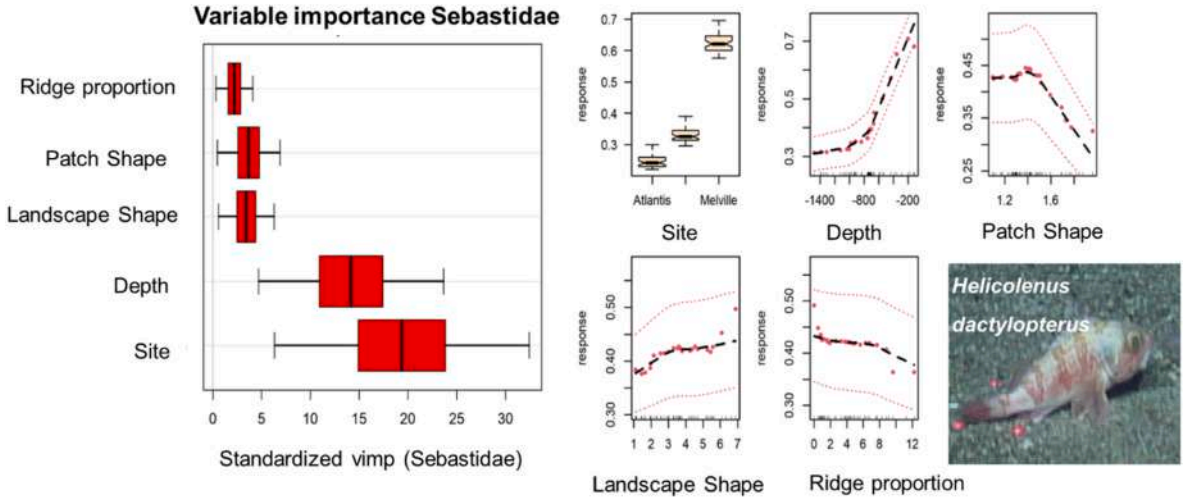


Fig. 8. Example output of variable importance (left panel) and effect of predictor variables (right panel) on the abundance of Sebastidae. Outputs for other families can be found in Appendix E.

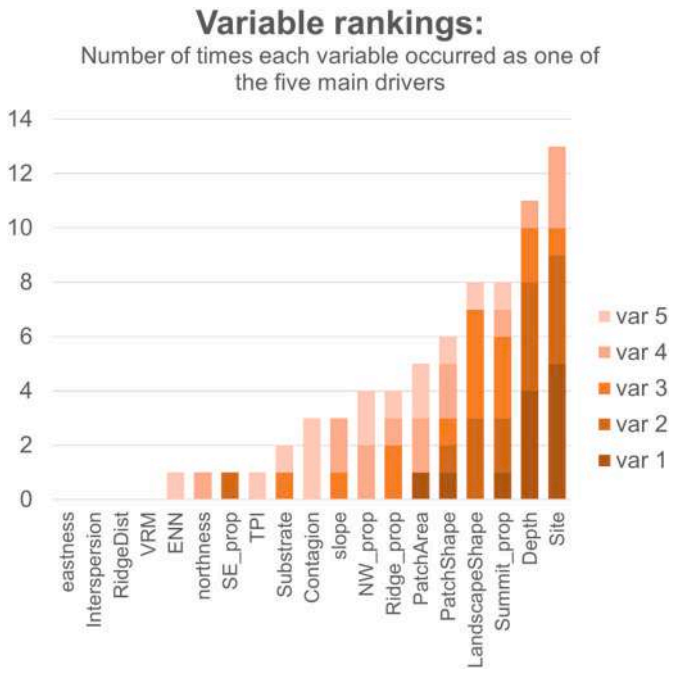


Fig. 9. Variable rankings (number of times each variable occurred as one of the five main drivers) obtained from multivariate regression trees.

et al., 2009). A positive relationship between patch area and abundance was found for some summit-associated aggregating fish families at Atlantis (Pentacerotidae, Centrolophidae). These larger patch areas indicate increased availability of spatially continuous summit habitat, and support larger feeding aggregations. In contrast, assemblage diversity and some bottom-dwelling twilight zone and bathyal families (Etmopteridae, Gempylidae) relate to small patch areas in more aggregated seascapes. These results fit the perspective of niche theory, which predicts more diverse and connected seabed environments support higher biological diversity (Harris, 2012; Ismail et al., 2018). This might be relevant for bottom-dwelling families that utilise their local environment for different activities (e.g. feeding, resting).

More complex patch shapes were expected to negatively influence fish assemblage characteristics due to edge effects: the abrupt changes in physical structure at the transition zones between patch types. Indeed, away from the summit, rockfish and scorpionfish (Sebastidae, Scorpaenidae) were associated with simple patch shapes. These solitary fish are bottom-dwelling and have low activity levels, and therefore might depend on contiguous environmental conditions. In contrast, complex patch shapes positively influenced abundance and richness of several other families (e.g. Pentacerotidae, Oreosomatidae). This matches literature from coastal habitats, suggesting that fish biodiversity may show positive responses to edges (Boström et al., 2011). In seamount environments, complex patch shapes may, for example, be linked to the presence of complex shaped crest and ridge features. These complex features may be important demersal fish by protecting from predation, or enhancing foraging opportunities by concentrating food particles (Genin and Dower, 2008; Read and Pollard, 2017). Additionally, more complex patch shapes may create a more heterogeneous environment, that following niche theory, would be positively related to richness and diversity.

Aggregated landscape characteristics were expected to positively influence abundance because of structural connectivity provided by spatial continuity (Grober-Dunsmore et al., 2007). Indeed, spatial continuity, measured by the landscape shape index, was the main configuration metric influencing fish families and overall abundance and diversity. It is important to reiterate that the landscape shape index was highly collinear with landscape diversity, evenness, patch abundance and richness, and splitting index, and therefore also functions as a proxy of these metrics. The effect of landscape shape index varied between families, which also explains the non-linear relationship of landscape shape to overall fish abundance. Spatially contiguous seascapes appeared mainly important for the twilight zone associated fish families found at Atlantis (including Pentacerotidae, Squalidae, Berycidae, Centrolophidae). These families dwell over summits for feeding and/or hunting, and increased availability of spatially contiguous summit habitat might therefore support larger abundances of these families. In contrast, bottom-dwelling Sebastidae appeared correlated to higher values of the landscape shape index. These indicate increased patch richness, and bottom-dwelling families might benefit from multiple patch types in their direct surroundings to support their low activity levels. Similarly, higher values of contagion and nearest neighbour index were important for bottom-dwelling Moridae at Coral Seamount, that use multiple habitats and may benefit from increased proximity of these habitats.

Interpreting fish-habitat associations using seascape metrics requires consideration of scale-dependent responses. Broad-scale habitat maps were deemed appropriate as many of the fish families targeted for

fishing are highly mobile and use their environment over extended areas (Shotton, 2006). However, producing habitat maps at scales ecologically relevant for the fish families might further improve knowledge gained. For example, "summit" was classified as one feature, but within the broad-scale summit feature there can be features such as boulders that might be ecologically relevant for some species (Bo et al., 2021). Here, we did not account for such finer scale interactions, as the resolution of the input data did not allow to resolve such detail. However, "substrate type" was incorporated at a finer scale (average of photo frames within transects) as fine-scale substrate features have been shown to strongly influence deep-water fish communities (Quattrini et al., 2012; Ross and Quattrini, 2007) but was not a major predictive variable.

4.3. Final considerations

4.3.1. Importance

Conservation and fishery management of remote deep-sea ecosystems such as seamounts rely partly on proxies of habitat suitability to estimate ecologically important areas (Clark et al., 2012; Moore et al., 2016a). This study highlighted that the regional environment, predominantly seamount site and depth, determines the boundary conditions for more local effects of seascape composition, configuration and terrain structure on fish assemblages. A previous hierarchical biophysical classification of seamounts incorporating summit depth in the southern Indian Ocean already assigned Coral, Melville and Atlantis belonging to different biogeographic classes along the SWIR (Clark et al., 2011); see also Sutton et al. (2017) for the twilight zone). This is consistent with the findings of this study that commercial assemblages differed significantly between the studied seamounts and depth zones. These findings have implications for establishing representative benthic or marine protected areas in this region.

At the scale of individual seamounts, current frameworks in seamount management already recognise the importance of particular broad-scale habitats – seascape composition-such as the summit (Clark and Dunn, 2012). This study indicates the spatial characteristics and configuration of these habitats, in particular their shape and spatial continuity, are equally ecologically important. Considering spatial configuration could be valuable to achieve a representative network of protected areas incorporating seamounts varying in spatial characteristics of morphology (Clark et al., 2011).

Methodologically, this study also demonstrated that patch-based metrics provided a strategy to test new hypotheses related to species diversity in the deep sea, although this study did not provide conclusive results. Additionally, patch-based metrics had larger predictive power than continuous terrain metrics commonly used in developing proxies for deep-water biodiversity. The geomorphological habitat map from which composition and configuration metrics were derived in this study, was however constructed based on geomorphological characteristics, which incorporate terrain structure.

4.3.2. Study limitations

Although seascape composition, configuration and terrain structure proved useful to disentangle fish-habitat associations with different sets of environmental characteristics, they were derived from a limited number of observations and highly site-specific. This was indicated by the differences in performance of random forests and regression trees. Whereas both exhibited high explanatory power, predictive power was limited, limiting universal conclusions on the effect of seascape composition and configuration on seamount-associated fish. Additionally, there are biases associated with all fish sampling methods, including video transects conducted with ROVs (Sward et al., 2019). Specifically, conducting video transects using an ROV may result in avoidance or fleeing behaviour of fish (Stoner et al., 2008), and underwater vehicles could be less successful at recording fish species on steep slopes and hiding within crevices (Osuka et al., 2021), compromising the ability to record all individuals originally present at a location.

Additionally, the lack of extensive surveys on all seamount habitats in this study limited the ability to identify assemblages and their drivers on seamount flanks. We envision future studies can expand on this knowledge and therefore recommend further adoption of seascape metrics. Further, finer-scale data, both in taxonomic resolution and spatial resolution might provide additional insight in characteristics important for individual species targeted by fisheries. Indeed, finer scale taxonomic data may be more accurate for deep-sea habitat suitability modelling (Bowden et al., 2021) and fish-habitat associations are dependent on spatial scale and environmental context (Anderson et al., 2009).

5. Conclusion

As few seamount ecosystems have been studied in detail, there remains a need to increase our understanding on how seamount habitat heterogeneity supports biology and ecology (Rogers, 2018). Using seascape ecology metrics rarely used in deep-water environments to study fish-habitat associations at SWIR seamounts, this study revealed:

1) Fish assemblages were primarily driven by depth and site, and seascape composition, configuration and terrain structure explained associations within sites and depth classes
2) Demersal fish responded to unique combinations of seascape composition, configuration and terrain structure depending on their traits, with some overlap between families found in the same sites and depth zones.
3) Broad-scale habitat features, specifically the summit and the proportion of ridge habitat, and their spatial continuity and shape, were main drivers of assemblage characteristics
4) Seascape composition and configuration metrics had higher explanatory power than commonly used terrain structure metrics.

Based on these findings, we recommend that future studies looking at habitat suitability over the full spectrum of seamount morphology continue to consider the spatial composition and configuration of seascapes.

Author contributions

DS- conceptualization, methodology, formal analysis, writing – original draft, writing-review & editing. TM: formal analysis (fish ID). ADR: Funding acquisition, field data collection, formal analysis (fish ID), writing-review & editing. VH, SP, LW: supervision, writing-review & editing. MT: Field data collection, writing-review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Biological dataset has been made available in the Supplementary Material. Environmental data is available upon request

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Appendix A. Supplementary data

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E.4 *Geomorphological drivers of deeper reef habitats around Seychelles*

Coral Reefs
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REPORT

Geomorphological drivers of deeper reef habitats around Seychelles

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Abstract Mesophotic (30–150 m) and rariphotic (150–300 m) deeper reef habitats are important from an ecological and conservation perspective, yet remain understudied. Key knowledge gaps exist on the environmental patterns and processes that drive and shape their geographical distributions. Understanding these is particularly important for regions as the Western Indian Ocean, where deeper reefs are poorly known but support food security and host economically important species. Spatial predictive models of assemblage occurrences, using terrain variables as predictors, offer a solution to address knowledge gaps around deeper reef distributions. We identified relationships between seafloor geomorphology, quantified at multiple scales, and sessile benthic assemblages in four atoll seascapes in Seychelles using terrain models derived from high-resolution multibeam sonar and underwater video surveys. Using random forests and boosted regression trees, we demonstrated that terrain derivatives extracted over multiple scales perform as reliable predictors of deeper reef assemblages. The most influential environmental predictors were depth, distance to shore, topographic complexity, slope and curvature and substrate characteristics. The relative importance of predictors was explained by assemblage functional characteristics. Assemblage–environment relationships were used to produce probability distribution maps that showed similar distributional patterns for identified assemblages across locations, with high occurrence probabilities linked to complex geomorphological structures. Our results help contribute to a consistent baseline understanding of the relationship between seascape structure and mesophotic reef ecosystems in this area. Complex geomorphological structures, including terraces and paleoshorelines, supported high densities of mesophotic assemblages and could be considered priority habitats for management.

Keywords Mesophotic coral ecosystems · Geomorphology · Habitat suitability modelling · Seychelles

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Introduction

Mesophotic coral ecosystems (MCEs, 30–150 m) and rariphotic habitats (150–300 m) are widespread in tropical and subtropical regions (Pyle and Copus 2019). These "deeper reefs" host biodiverse communities of interest to conservation (Soares et al. 2020), provide key ecosystem functions and services including food provision and refuge for some depth-generalist reef species affected by climate change-induced rising sea temperatures and/or shallow-water disturbances (Holstein et al. 2019).

Although deeper reef research is increasing globally, for many tropical regions the distribution and biological data

from these habitats is unavailable due to the financial, technological and operational constraints of underwater surveys beyond the depth limits of most airborne sensors and conventional SCUBA diving (> 30–50 m depth) (Woodall et al. 2018). Consequently, the environmental factors shaping deeper reef assemblages remain poorly described for most areas (Turner et al. 2017). This is particularly acute for the Western Indian Ocean (WIO) region where there is very little information on deeper reefs (Pyle and Copus 2019; Osuka et al. 2021). Improving our understanding of the environmental factors that drive deeper reef ecosystems is important for ecosystem-based management approaches aiming to identify seascape features important for ecosystem health and functioning (Hinderstein et al. 2010; Bridge et al. 2020).

Seabed topography influences habitat suitability and is a demonstrated driver of benthic species distributions (Wilson et al. 2007). Geomorphology influences deeper reef occurrence and distribution through its effects on habitat structure and substrate characteristics and by mediating biotic and abiotic processes such as hydrodynamic flows, turbidity and sedimentation (Kahng et al. 2010; Locker et al. 2010; Sherman et al. 2019). The quantification of seabed structural patterns from bathymetric surveys combined with data from visual surveys of deeper reefs has enabled the application of predictive distribution modelling as a tool to address biogeographical and ecological knowledge gaps (Guisan et al. 2013; Costa et al. 2015). Predictive distribution models that result in maps of expected habitat suitability have become critical tools to inform the design of effective conservation measures (Bridge et al. 2020). The majority of deeper reef distribution modelling studies have focused on a dominant mesophotic species or taxon (Costa et al. 2015; Veazey et al. 2016; Silva and MacDonald 2017). These efforts might not always be representative, as deeper reefs often comprise diverse benthic communities, including corals, sponges and algae with no single dominant group or taxon (Kahng et al. 2010; Bridge et al. 2011a; Turner et al. 2017). Instead, assemblage-based predictive models can incorporate multiple species, including low abundance species in a single model (Ferrier and Guisan 2006; Piechaud et al. 2015).

Few studies globally study the occurrence of both MCE and rariphotic megabenthos at the assemblage level (e.g. Stefanoudis et al. 2019), and there are even fewer that relate assemblages to local geomorphology. To explain and predictively map the spatial distribution of deeper reefs around remote WIO atolls, this study classifies and predictively models the distribution of benthic assemblages using digital bathymetric models and underwater video. The study objective was to determine if seabed terrain structure quantified at multiple scales can act as a reliable spatial proxy for predicting deeper reef assemblage distribution. We addressed this objective by: (1) clustering biological observations to categorize assemblage composition at each site; (2) testing assemblage associations with multiscale terrain metrics and their relative importance in driving assemblage occurrence and distribution; (3) defining habitat preferences for these assemblages based on metric ranges identified; and (4) identifying geomorphological features that may represent priority habitats for conservation by predicting the spatial distribution of deeper reef assemblages.

Methods

Study area

Seychelles is an archipelagic state in the Western Indian Ocean. This study focused on four coral atolls: three in the Amirantes island Group: Desroches (DES), St. Joseph (StJ) and Poivre (POI), and one in the Aldabra Group: Aldabra (ALD) (Fig. 1a). Biological ground-truthing and multibeam echosounder data were collected at every site (Fig. 1b–e) between March and April 2019 during Seychelles First Descent (Woodall and Rivers 2019).

Biological data collection and preparation

At each site, three replicate 250 m long video transects were collected at four target depths (~ 30 m, 60 m, 120 m and 250 m) using stereo-sets of video cameras (Paralenz Dive-Camera +) mounted on a submersible (Triton 1000/2). This depth-stratified sampling design was chosen to balance various science objectives of the expedition. Photo frames were extracted every 30 s from video data, and each photo frame was linked to a geographical position (latitude, longitude and depth) corresponding to submersible location. The best quality photograph of each stereopair was then selected for biological and substrate data annotation. Photo frames were excluded from the analysis if no USBL positioning data were available, if photo quality was inadequate for video annotation (low light, blurry, obstructed) and when submersible distance from the seabed was too great to allow positive identification of benthos (= photos covering an area > 8 m^2).

With the image analysis software TransectMeasure from SeaGIS (Seager 2014), retained photo frames were annotated using twenty random points per m^2 classified as either a substrate type or a living organism. Sessile megabenthos was placed into morphotypes (= morphologically similar specimens) identified to the lowest possible taxonomic level, which in most cases was genus or family (Fassbender et al. 2021). For each photo frame, substrate classifications were averaged and merged according to the majority rule (> 50% of points) to hard (bedrock, rubble, boulders, cobbles—class 1), mixed (when substratum types occurred in equal proportions, class 2) or soft (mud,

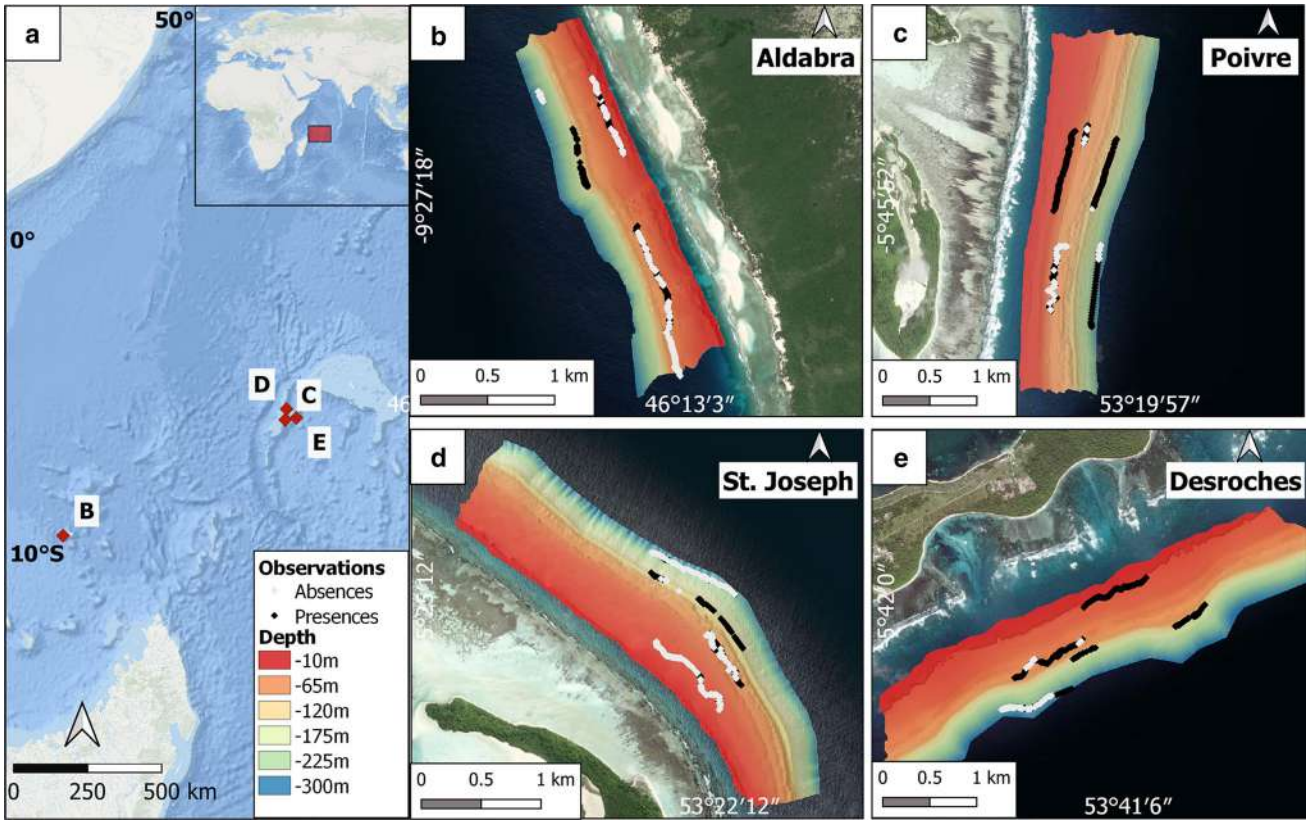


Fig. 1 Research locations within the Seychelles archipelago (**a**) and bathymetry and submersible video transect tracks at each study site (**b**–**e**). White and black dots indicate absences and presences of deeper reef assemblages, respectively. Area surveyed at each site was approximately 2km^2

sand, sediment—class 3) substratum Using this method, 350–500 annotated photographs were extracted per site. When no organisms were visible in the photo an absence was recorded. The total surface area annotated averaged 749 m^2 per survey site (Aldabra: 931 m^2, St Joseph: 595 m^2, Poivre: 628 m^2 and Desroches: 843 m^2).

Hierarchical agglomerative clustering based on Bray–Curtis dissimilarity and Ward's minimum variance method was conducted to identify clusters of co-occurring taxonomic groups at each site, using the packages *vegan* (Oksanen et al. 2018) in R version 3.5.1 (R Core Team 2018). The optimum number of clusters for each site was determined by maximizing Dunn's index (Dunn 1973). Clustering results were visualized using non-metric multidimensional scaling (nMDS) plots and PERMANOVA was used to confirm their statistical significance ($p < 0.05$). The contribution of recorded taxa to clusters per site was assessed using permutational Dufrene-Legendre indicator species analysis (Dufrene and Legendre 1997) in R package *indicspecies* (Cáceres and Legendre 2009). Each photo was assigned an assemblage class, as defined by the clustering analysis.

Environmental predictors

Bathymetry and acoustic backscatter data were collected at each site between 0 and 300 m depth, using a Teledyne Reson Extended range SeaBat T50-P multibeam echosounder and the Teledyne PDS acquisition software. Qimera (QPS) software was used to process and grid the bathymetric data to 2 × 2 m resolution. Backscatter data were processed using the FMGeocoderToolbox (Fledermaus™ software, QPS). Despite post-processing, bathymetry contained some small artefacts at Desroches and Poivre and backscatter data was oversaturated (artificially inflated backscatter intensity) in areas beyond 150 m depth at all sites. As oversaturation was only a problem for these deeper depths, backscatter was nevertheless included as predictor variable.

Ecologically relevant terrain derivatives were extracted in ArcMap 10.6 using Benthic Terrain Modeller (BTM) (Walbridge et al. 2018) and in R using the *raster* (Hijmans 2017) and *spatialEcology* (Evans 2017) packages. Terrain derivatives were chosen to represent four broad geomorphological classes: slope, orientation, curvature and terrain variability (Wilson et al. 2007, Table 1). Parameters

Table 1 Predictor variables explored and retained to quantify seascape structure. The table indicates their ecological relevance, method of extraction and spatial scales retained for analysis

Class	parameter	Unit	Ecological relevance	Scale (m)	Calculated in	Retained for analysis
Depth	Water depth	Meters	Relates to several environmental parameters including light penetration, temperature and productivity	2×2, 10×10, 25×25	Bathymetry	Yes
Slope	Slope	Degrees	Measures elevational change, which is a proxy for substratum, local hydrodynamic regime and sedimentation	2×2, 10×10, 25×25	R raster	Yes
Orientation	Aspect Measured as eastness (sinasp) and northness (cosasp)	Radians	Reflects the orientation of the seabed, which is a proxy for current exposure		BTM (ArcMap 10.6)	Yes
Curvature and relative position	Total curvature (curv), plan curvature (curvature_pl) and profile curvature (curvature_pr)	Measured in 1/100th of a z-unit (m) in ArcGIS. 0 indicates a flat surface, positive values indicate convex surface and negative values indicate a concave surface	Second derivative of bathymetric surface, Measures the convexity/concavity of the seascape, which gives information on the orientation and relative elevation of the surface	2×2, 10×10, 25×25	ArcGIS 3D Analyst	Yes
			Plan curvature is the second derivative only evaluated perpendicular to slope (horizontal plane), which influences flow convergence and divergence			Yes
			Profile curvature is the second derivative only evaluated parallel to the slope (vertical plane), which affects flow speed and resulting erosion and deposition			Yes
	Bathymetric Position Index (BPI)	Mean elevation value in m within analysis neighbourhood	Indicates whether an area is part of a positive or negative feature of the surrounding terrain, which is a proxy for exposure or shelter opportunities		R spatialEco	No, collinear with curvature

Table 1 (continued)

Class	parameter	Unit	Ecological relevance	Scale (m)	Calculated in	Retained for analysis
Terrain variability	Rugosity	Unitless ratio	Measures the ratio between the three-dimensional surface area and the planar area of the surface, influencing habitat heterogeneity	2×2, 10×10, 25×25	BTM (ArcMap 10.6)	No, collinear with slope and TRI
	Arc-chord Rugosity (ACrug)	Unitless ratio	The ratio of surface area to planar area of best fit, which decouples rugosity from slope, unlike the normal rugosity calculation		BTM (ArcMap 10.6)	Yes
	VRM—vector ruggedness measure	Dimensionless value ranging from 0 (no variation) to 1 (high variation)	Measures the variation in the three-dimensional orientation of grid cells within a neighbourhood as proxy for habitat heterogeneity		R spatialEco	No, collinear with arc-chord rugosity and slope of slope
	Terrain Ruggedness Index (TRI)	Meters of elevation difference between grid cells	Reflects local variation in seabed terrain, associated with changes in habitat complexity		R spatialEco	No, collinear with slope and rugosity
	Slope of slope	Degrees of degrees	Measures the change of the slope gradient as measure of terrain variability		R raster	Yes
Substratum	Backscatter (BS)	dB	Measure of the seabed reflectivity, which is a proxy for substratum type	2×2, 10×10, 25×25	NA	Yes
	Substratum type (created using random forest classification of other terrain variables)	Classified values	Classified as hard (class 1), mixed (class 2) or soft (class 3). Substratum characteristics affect organism settlement and colonization	2×2	R raster, caret	Yes
Geographic	Distance to shore	m	Geographic proxy for variables relevant for deeper reef recruitment and growth, including current regime and turbidity influencing light availability, and sea surface temperature	2×2	ArcMap 10.6	Yes. Although distance to shore was expected to be coupled with depth, Pearson correlation was lower than |0.7|

describing substrate type and geographic position were also quantified (Table 1). Although correlation between assemblage occurrence and sampling depth is expected as a result of the sampling design, depth was included as a continuous predictor to enable meaningful spatial predictions outside of sampling depths. Where variables exhibited high collinearity (Pearson correlation >|0.7|), the variable allowing for more intuitive ecological interpretation was retained (Dormann et al. 2013). The substrate classes identified in the annotation process (soft, mixed, hard) were used as ground-truthing for a random forest classification (Breiman 2001) using the non-collinear predictors excluding backscatter.

To investigate the influence of spatial scale on the relationships between terrain morphology and assemblage structure, terrain derivatives were extracted from bathymetry resampled to three spatial resolutions (2 m, 10 m, 25 m). The highest gridding resolution of bathymetry data determined the finest spatial scale (2 m). The appropriate broad scale was determined using Dragut's Estimation of Scale Parameter (ESP) Tool (Drăguţ et al. 2010), where a decline in Rate of Change of Local Variance (ROC-LV) curves was observed at a resolution of 25 m. Derivatives were also calculated at 10 m resolution to account for intermediate-scale effects and following resolutions used in other mesophotic reef studies (Costa et al. 2015; Sterne et al. 2020). Although variables at multiple scales exhibited collinearity, these were retained to account for possible multiscale effects of predictors on assemblage occurrence and distribution. Machine learning algorithms used in this study are less sensitive to collinearity and can be parameterized to avoid overfitting while dealing with several variables and interactions (Costa et al. 2015).

Model selection, building and evaluation

Random forests (RF) (Breiman 2001) and boosted regression trees (BRT) (Friedman 2001) were used to generate spatial predictive models. RFs and BRTs are machine learning algorithms adept at modelling complex nonlinear responses, allowing interactions between predictor variables and effectively filtering out irrelevant predictors (Elith et al. 2008).

R packages *randomForest* (Liaw and Wiener 2002) for RF models and *gbm* (Ridgeway 2017) for BRT models were implemented through the package *caretEnsemble* (Deane-Mayer and Knowles 2016). The model building process was identical for each assemblage cluster and site. We created a presence-absence dataset for each assemblage, where observations assigned to that assemblage through clustering were scored as presences (Table 2). We subsequently extracted the values of predictor variables from the raster cell corresponding to the geographic x, y, z location of each photo frame. We optimized the number of trees and number of variables available for splitting at each node (mtry) in RF models, and the number of trees, interaction depth (complexity) and shrinkage (learning rate) for BRT models. The best model was selected using the smallest value for the mean absolute error (MAE). Our evaluation dataset was obtained by structured sub-sampling of the training data set during the ten-fold cross-validation process. We conducted a performance assessment by running ten resamples of the produced model.

For each model, we evaluated: (1) model performance in (a) discrimination capacity, using the area under the curve of the receiver operating characteristic (AUC-ROC), where a value of 0.9–1 indicates excellent performance, a value of 0.7–0.9 good performance and a value of 0.5 a performance no better than that expected by chance; (b) reliability, using the mean absolute error (MAE) which ranges from 0 to 1, with 0 corresponding to a model that is a perfect output predictor; (c) spatial autocorrelation in model residuals and (d) visual accuracy; (2) the contribution of predictors to each model using variable importance analysis; (3) habitat preferences for each assemblage with partial dependence plots (Milborrow 2020) and density plots (Bowman and Azzalim 2018); and (4) predicted assemblage occurrence and distribution over the entire site.

Results

Cluster composition

Cluster analysis resulted in four assemblage clusters for each site (Table 2, Fig. 2, Online Resource 1–1), which despite some overlap between assemblages 1–3 (Fig. 3), all differed significantly in composition (PERMANOVA $p < 0.001$, Online Resource 1–2). Indicator species analysis performed on these assemblage clusters demonstrated that, although the exact taxa composition of each assemblage cluster differed per site, they corresponded to similar biological zones linked to sampling depth (Table 2, Online Resource 1–3). Assemblage 1 (30–60 m, Fig. 2a) contained scleractinians and zooxanthellate octocoral, macroalgae and sponges. Assemblage 2 (60 m, Fig. 2b) is dominated by azooxanthellate octocoral with diverse morphologies, scleractinians showing depth adaptations (e.g. dominance of plating morphologies that enhance monodirectional light absorption) and some antipatharians. Assemblage 3 (120 m, Fig. 2c) consisted mainly of azooxanthellate octocoral fans and encrusting organisms, most notably crustose coralline algae (CCA) and Porifera. Reef-building species were absent from assemblage 4 (250 m, Fig. 2d), which consisted of sea urchins and sea stars and occasionally hydrocorals (Stylasteridae). Indicator species analysis also revealed generalist taxa that occurred across multiple assemblage clusters, most notably Demospongiae sp. 2, Hydrozoa spp. and Corallinales spp; however, it is worth noting that these are coarse

Table 2 Taxa significantly ($p < 0.05$) associated with each cluster per site, ordered by indicator value. Taxa are described in Fassbender et al. (2021)

Assemblage	St Joseph	Desroches	Poivre	Aldabra
1: 30–60 m: Scleractinia, Alcyonaceae, Chlorophyta, Demospongiae	*Porites* spp. *Halimeda* spp. *Favites* spp. *Dipsastrea* spp. *Spheciospongia* sp. 1 *Echinophyllia* spp. *Leptoseris* spp. *Stylissa carteri* *Sinularia* spp.	*Halimeda* spp. *Porites* spp. *Pachyseris* spp. *Stylissa carteri* *Fungiidae* sp. 2 *Favites spp.* *Fungiidae* sp. 1 *Lobophytum* spp. *Montipora* spp. *Acropora* spp. *Goniastrea* spp.	*Halimeda* spp. *Acropora* spp. *Fungia* spp. *Porites* spp. *Microdictyon* spp. *Fungiidae* sp. 1 *Codium* spp. *Leptoseris spp.* *Haliclona* sp. 2 *Udotea spp.* *Sarcophyton* spp.	*Theonella* spp. *Clathria* sp. 1 *Spheciospongia* sp. 1 *Stylissa carteri* *Porites* spp. *Lobophyllia* spp. *Montipora* spp. *Favites* spp. *Pachyseris* spp.
2: 60 m: Alcyonaceae, Scleractinia, Antipatharia, Demospongiae	*Ellisella* spp. *Dichotella* spp. *Hydrozoa* spp. *Cupressopathes* spp. Plexauridae sp. 8	Plexauridae sp. 14 Plexauridae sp. 9 *Ulva* spp. *Viminella/Junceella* spp. Alcyonaceae spp. Plexauridae sp. 8 *Nicella* spp. *Solenocaulon* spp. *Ellisella* spp. *Dendronephthya* sp. 1 *Annella* spp.	Ellisellidae sp. 1 Demospongiae sp. 3 *Antipatharia* spp. *Porites* spp. *Dendronepththya* spp.	*Iotrochota nigra* *Ellisella* spp. *Spheciospongia* sp. 2 *Solenocaulon* spp. *Haliclona* sp. 2 Plexauridae sp. 3 *Tetilla* sp. 1
3: 120 m: Rhodophyta, Demospongiae, Antipatharia, Alcyonaceae	*Oceanapia* spp. Demospongiae sp. 1 Plexauridae sp. 2 *Tetilla* sp. 1 Corallinales spp. Alcyonaceae spp. *Ophidiasteridae/ Echinasteridae* spp.	*Heteronardoa diamantinae* Plexauridae sp. 2 *Oceanapia* spp. Hydrozoa spp. *Tetilla* sp. 1	Demospongiae sp. 1 *Tetilla* sp. 1 *Viminella/Junceella* spp. Plexauridae sp. 2 *Oceanapia* sp.	*Corallistes* spp *Litophyton* spp *Viminella/Junceella* spp. *Nicella* spp. *Pachastrella* spp. Plexauridae sp. 2 Plexauridae sp. 6 *Astrogorgia* spp. Cidaroida sp1
4: 250 m: Echinoidea, Hydrozoa, Anthozoa	*Clypeaster* sp. Stylasteridae sp. 1 *Stylopathes* spp. *Mycropyga* spp.	*Clypeaster* spp. *Cidaroida* sp. 1 *Micropyga* spp.	*Clypeaster* spp. *Cidaroida* sp. 1 Decapoda spp. *Stylopathes* spp.	Actiniaria sp. 1 *Paguroidea* spp. Actiniaria sp. 2 Stylasteridae sp. 2 Decapoda spp.
Indicator taxa associated with multiple clusters: Rhodophyta, Demospongiae, Hydrozoa	*Viminella/Junceella* spp. (1 + 2), *Annella* spp. (1 + 2) Demospongiae sp. 2 (1 + 2)	Demospongiae sp. 2 (1 + 2 + 3) Corallinales spp. *(1 + 3)*	*Porites spp.* (1 + 2), Demospongiae sp. 2 (1 + 2 + 3), Corallinales spp. (2 + 3)	Demospongiae sp. 2 (1 + 2 + 3), Hydrozoa spp. (2 + 3), Corallinales spp. (2 + 3)

taxonomic identifications and hence include several species (Fassbender et al. 2021).

Model performance

All models showed good to excellent performance, with some site and assemblage-specific variation (Online Resource 2). With ROC-AUC values between 0.86 and 0.99 for RF (mean 0.95, sd 0.021) and 0.86 and 0.99 for BRT models (mean 0.94, sd 0.024), discrimination capacity was good to excellent for all models (Fig. 4a, c), and comparable between algorithms. Discrimination capacity was higher for assemblage 3 than other assemblages, with some site-specific variation without clear pattern. Like discrimination capacity, model reliability (Fig. 4 b, d) was good to excellent, with mean MAE ranging from 1.3% to 18.4% for RF (mean 9.2%, sd 1.8%) and from 1.6 to 18.2% for BRT models (mean 9.8%, sd 1.4%), comparable between algorithms. Model reliability was again high for assemblage 3 (mean MAE < 6%) and reduced for assemblages 1 and 2 (mean MAE up to 18%) with some site-specific variation. Although there was no significant residual spatial autocorrelation in BRT or RF models for assemblages 1, 2 and 3 calculated using Moran's I ($p > 0.05$), there was for assemblage 4 ($p < 0.05$) (Online Resource 2).

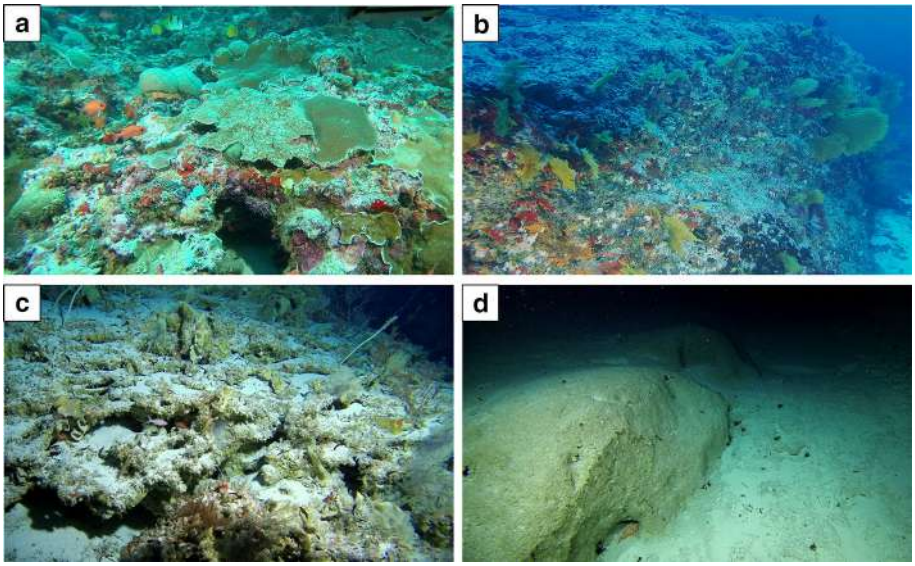


Fig. 2 Image **a**, **b**, **c** and **d** visualize representative examples of assemblage 1 (30–60 m), 2 (60 m), 3 (120 m) and 4 (250 m), respectively, at Aldabra

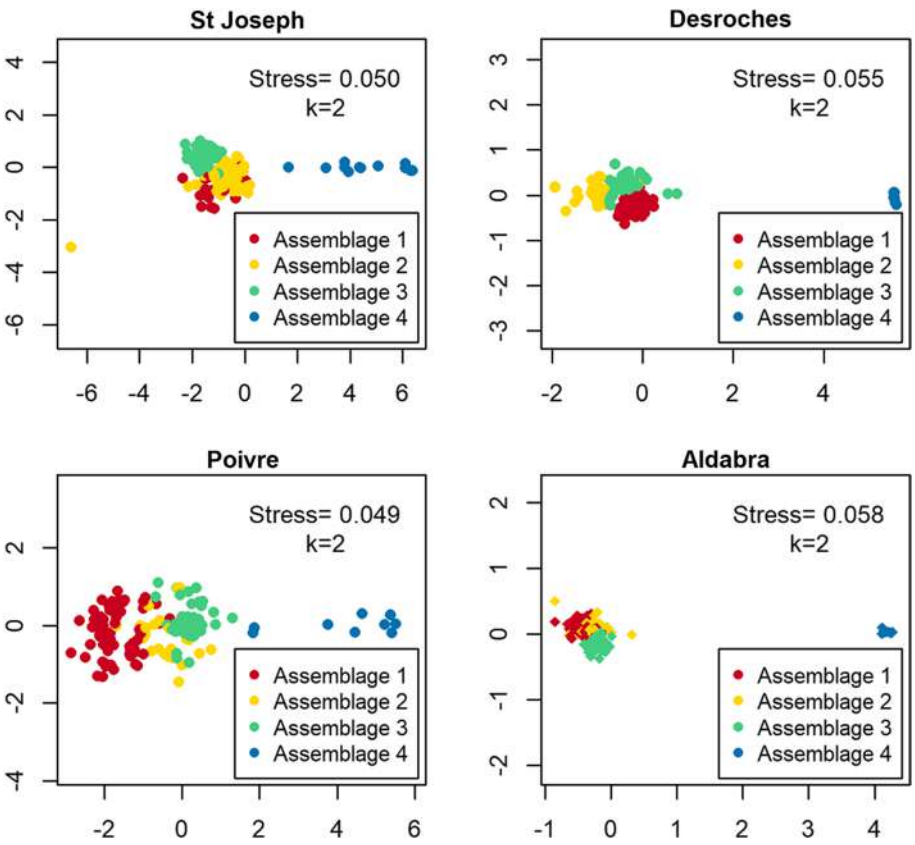


Fig. 3 nMDS plots visualizing the dissimilarity between observations from different assemblages

Predictor contributions to deeper reef distribution models

Overall, the main determinants of assemblage occurrence (measured by variable importance) were depth, distance to shore, arc-chord (AC) rugosity, curvature, slope and backscatter. Predictor variables calculated at 25 m and 10 m resolutions contributed more to the model than predictors calculated at the 2 m resolution, but were correlated. Primary predictors were consistent between model algorithms and geographical location. Variable importances showed that RF (Fig. 5a–d) models were often characterized by smaller contributions of multiple predictors extracted at different scales, whereas the relative contribution of individual

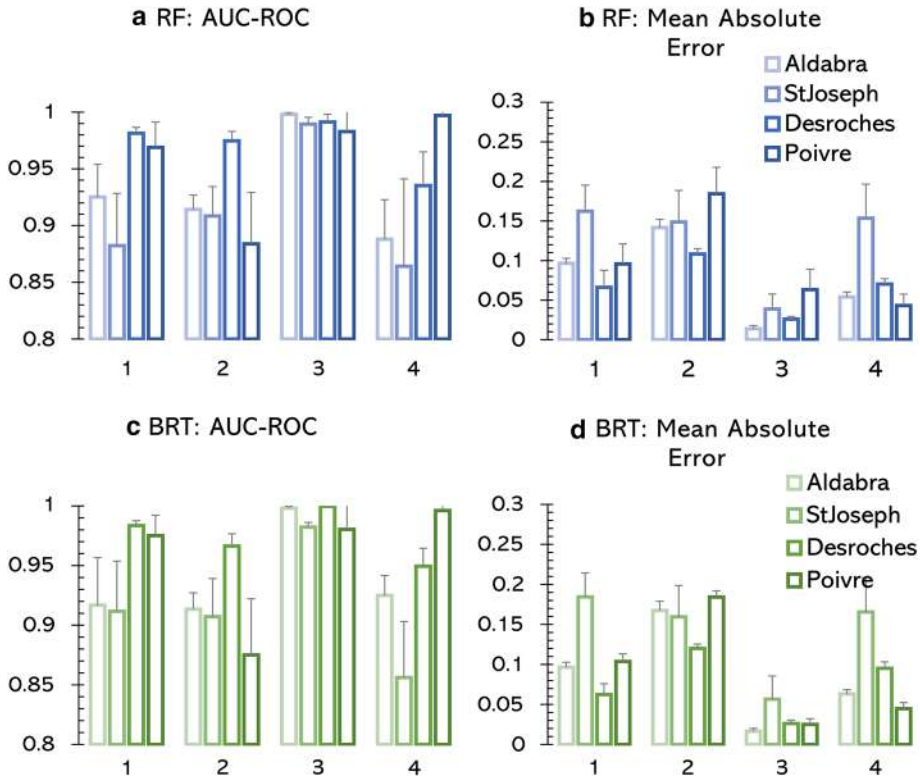


Fig. 4 Performance statistics per model for assemblage 1–4. Discrimination capacity was measured as area under the curve for the receiver operating characteristic (AUC-ROC) for both RF (**a**) and BRT (**c**). Accuracy was measured as mean absolute error for RF (**b**) and BRT (**d**). Standard errors were calculated as a function of 10 model iterations

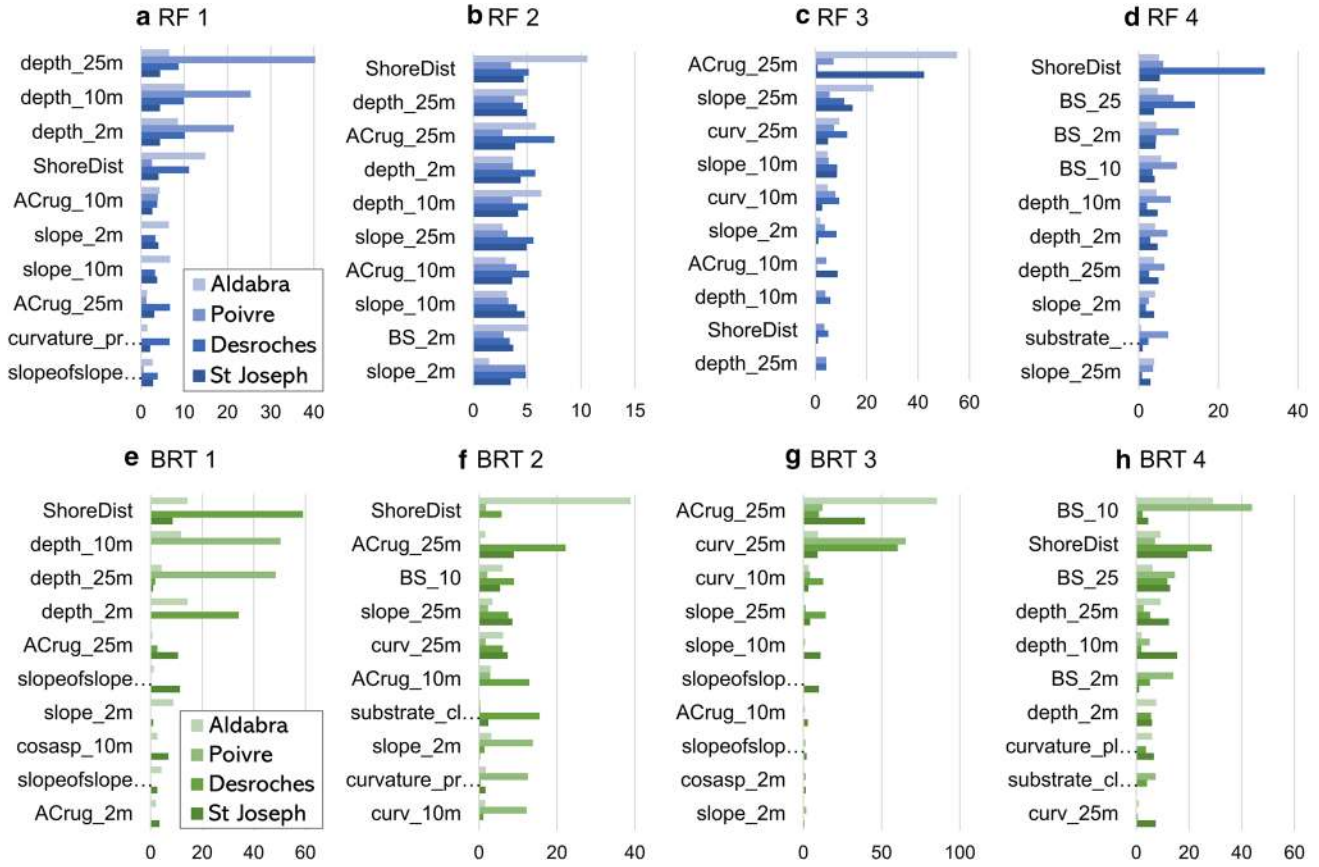


Fig. 5 Relative contribution of the ten main predictors per assemblage across sites, assessed for random forests (**a**–**d**) and boosted regression trees (**e**–**h**). Variable importance was calculated as the mean decrease in node impurity and standardized as a percentage

predictors was greater for BRT models (Fig. 5e–h) which filtered out predictors with low model contributions. The relative importance of these main predictors also varied with assemblage type.

The most important predictors of assemblage 1 were depth, distance to shore and terrain complexity (AC rugosity). Predictors associated with assemblage 2 also included depth, distance to shore and terrain complexity (AC rugosity), with slope and curvature important in BRT models. A smaller set of predictors contributed to the models of assemblage 3 and included curvature, terrain complexity (AC rugosity) and slope. Finally, depth, distance to shore and backscatter, which was oversaturated at these depths, contributed most to models of assemblage 4.

Predicted MCE habitat suitability

Deeper reef assemblage habitat preferences were derived from partial dependence plots (Online Resource 3) and density plots (Fig. 6, Online Resource 4). Partial dependence plots revealed that many key predictor variables had a non-linear relationship with model predictions. They also showed that key predictors (apart from depth and slope) exhibited variable multiscale effects on model predictions, with the effects of predictors extracted at fine-scale (2 m) often different from the effects of broad-scale (10 m and 25 m) predictors. Density plots were constructed using six broad-scale predictors that consistently contributed most across assemblages and models and revealed that assemblages were segregated by depth and distance to shore but mediated by terrain drivers important for individual assemblages.

Probability maps produced with the best performing models showed potential spatial distributions of each assemblage per site (Fig. 7 and Online Resource 5) and linked potential habitat characteristics identified using the partial dependence plots and density plots to geomorphological features.

Assemblages 1 and 2 were distributed over the insular shelf and exhibit high probabilities on elevated complex terrain as reef crests (Aldabra, Desroches), rocky ridges (Poivre) or terraces (St. Joseph). High probability densities of assemblage 1 were found closest to shore on either flat to gently sloping areas of low rugosity (AC rug < 1.01) on a mixed substrate (St. Joseph, Poivre, Fig. 6) or rugose (AC rug > 1.02) hard terrain such as ridges (Aldabra, Desroches). Across sites, high probability densities of assemblage 2 were linked to water depths extending to 75 m on slightly sloping (slope < 30°) or slightly curved terrain of hard to mixed substrate types. Assemblage 3 was environmentally distinct from other assemblages, with high probability densities on steeply sloping (slope > 40°), highly positively (St Joseph, Poivre, Aldabra) or negatively (Desroches) curved and rugose (AC rug > 1.02) terrain beyond depths of 100 m. These correspond to highly complex and sloping rocky ridges, including paleo-shorelines. Probability distributions for assemblage 4 were located on insular slopes and separated from those for assemblage 1, 2 and 3 and generally were higher in low rugose areas beyond 200 m furthest from shore on soft to mixed substrate (substrate class = 1 or substrate class = 2) consisting of sand or bedrock covered with sand and related to high backscatter intensities. However, the occurrence of assemblage 4 was environmentally not distinct from biological absences, as high probabilities of assemblage absences were found in similar environmental conditions as occurrences of assemblage 4. Regardless of site and model type used, spatial predictions of assemblage 4 were unreliable and strongly linked to oversaturated backscatter data beyond 150 m depth, particularly pronounced at Poivre and Desroches where assemblage 4 is predicted to occur in segregated sections that correspond to inflated values of backscatter intensity.

RF and BRT models show similar results in predicted assemblage locations but differ in the predicted extent and probability level. Probability distributions from BRT models appeared more sensitive to data artefacts or input data uncertainty. This was demonstrated in the probability maps of assemblage 1 at Desroches and Poivre (Online Resource 5) where bathymetric data < 70 m suffered from some artefacts.

Discussion

Mesophotic and rariphotic reef ecosystems are increasingly recognized as important biodiversity hotspots in the global tropics, but major knowledge gaps remain on the environmental factors that interact to influence assemblage structure, occurrence and resulting geographical distributions (Turner et al. 2019). By using an assemblage-level analysis, this study showed that deeper reefs consist of depth-separated assemblages that exhibit distinct responses to terrain variables.

Drivers and distribution of mesophotic assemblages

Across MCE assemblages, predicted distributions were strongly segregated by depth and distance to shore, both proxies of decreasing temperature and light penetration (Kleypas et al. 1999) that strongly influence MCE occurrence (Turner et al. 2017; Tamir et al. 2019). Moreover, substrate characteristics also drive and limit deeper reef occurrence: hard substrates provide settlement opportunities and may support more biodiverse deeper reef assemblages than mixed or soft substrata (Sherman et al. 2019). Assemblage–environment relationships for each individual assemblage appear related to their functional characteristics. Assemblage 1, composed of obligate zooxanthellate reef-building taxa (Table 2), is found in well-lit

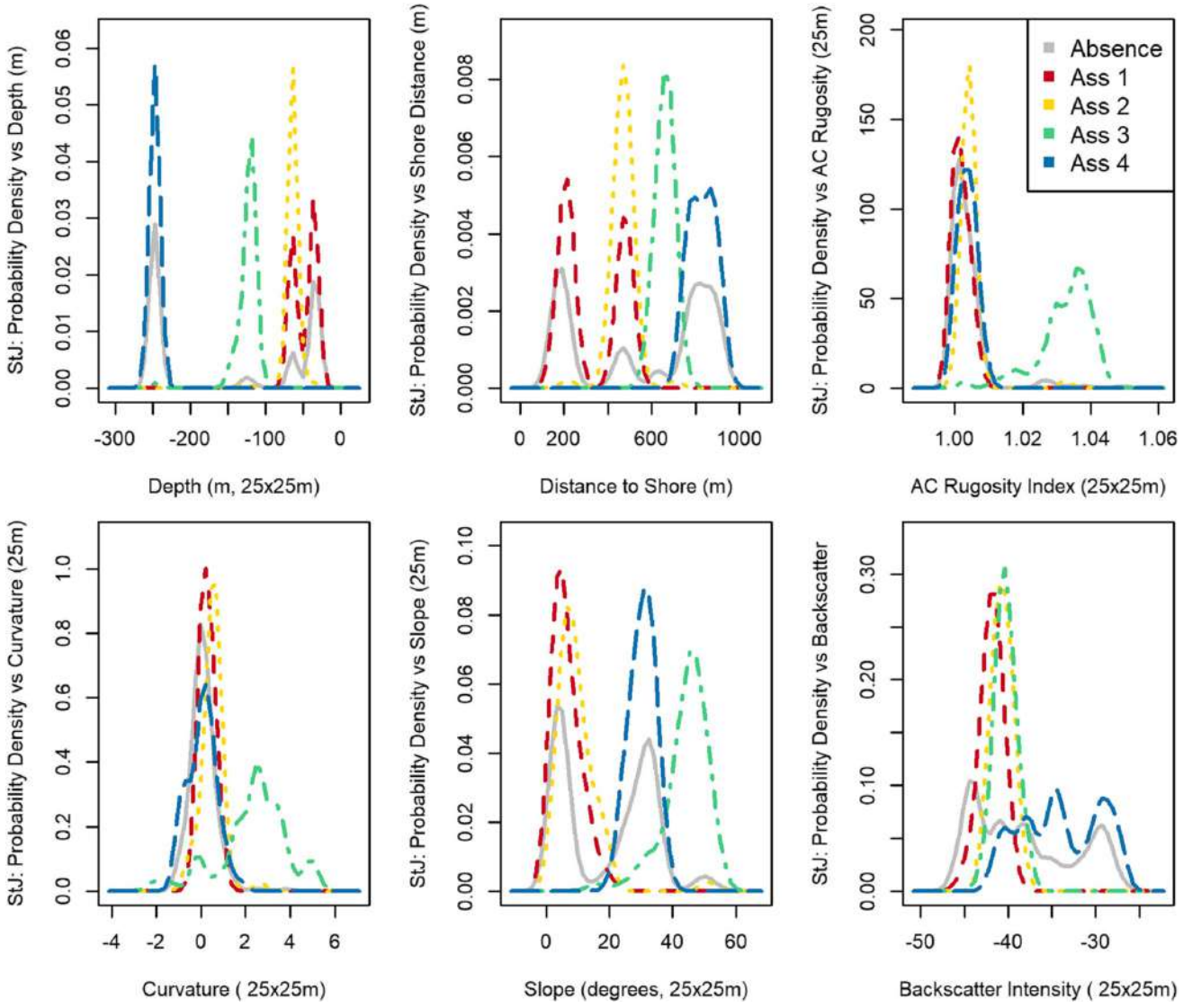


Fig. 6 Density plots of assemblage response to the consistently highest contributing predictors (depth, distance to shore, rugosity, curvature, slope and backscatter) extracted at the broadest resolution (25 m) at St Joseph. Density plots for Aldabra, Poivre and Desroches can be found in Online Resource 4

reefs between 30 and 60 m, which tend to be closest to island coastlines. Its occurrence was linked to complex terrain and hard substrate, but these values may be amplified as biogenic reef species found in assemblage 1 further contribute to the availability of complex terrain and hard substrate. Assemblage 2 contained both zooxanthellate and azooxanthellate species and is therefore in part associated with depths where sufficient light penetrates to enable photosynthesis. Assemblage 2 was also associated with slope and curvature which mediate hydrodynamic properties of water flow past the reef system, influencing food availability for heterotrophic suspension-feeding organisms (Locker et al. 2010; Bridge et al. 2011b; Sterne et al. 2020). Increased slope values may also shield taxa characterized by flattened morphologies found in assemblage 2 from heavy sedimentation (Ohlhorst and Liddell 1988; Kahng et al. 2010). Assemblage 3 consisted of encrusting morphotypes and azooxanthellate octocorals, and high habitat complexity strongly predicted its occurrence, mirroring results found in previous studies on mesophotic octocorals (Silva and MacDonald 2017). Structurally complex habitats may provide a variety of microhabitats that organisms can use for shelter and feeding, create additional settlement space for encrusting organisms and finally induce increased current flow that may bring food particles necessary for suspension-feeding octocorals (Pygas et al. 2020). The steep slopes and walls at ~ 120 m depth, where assemblage 3 was also found,

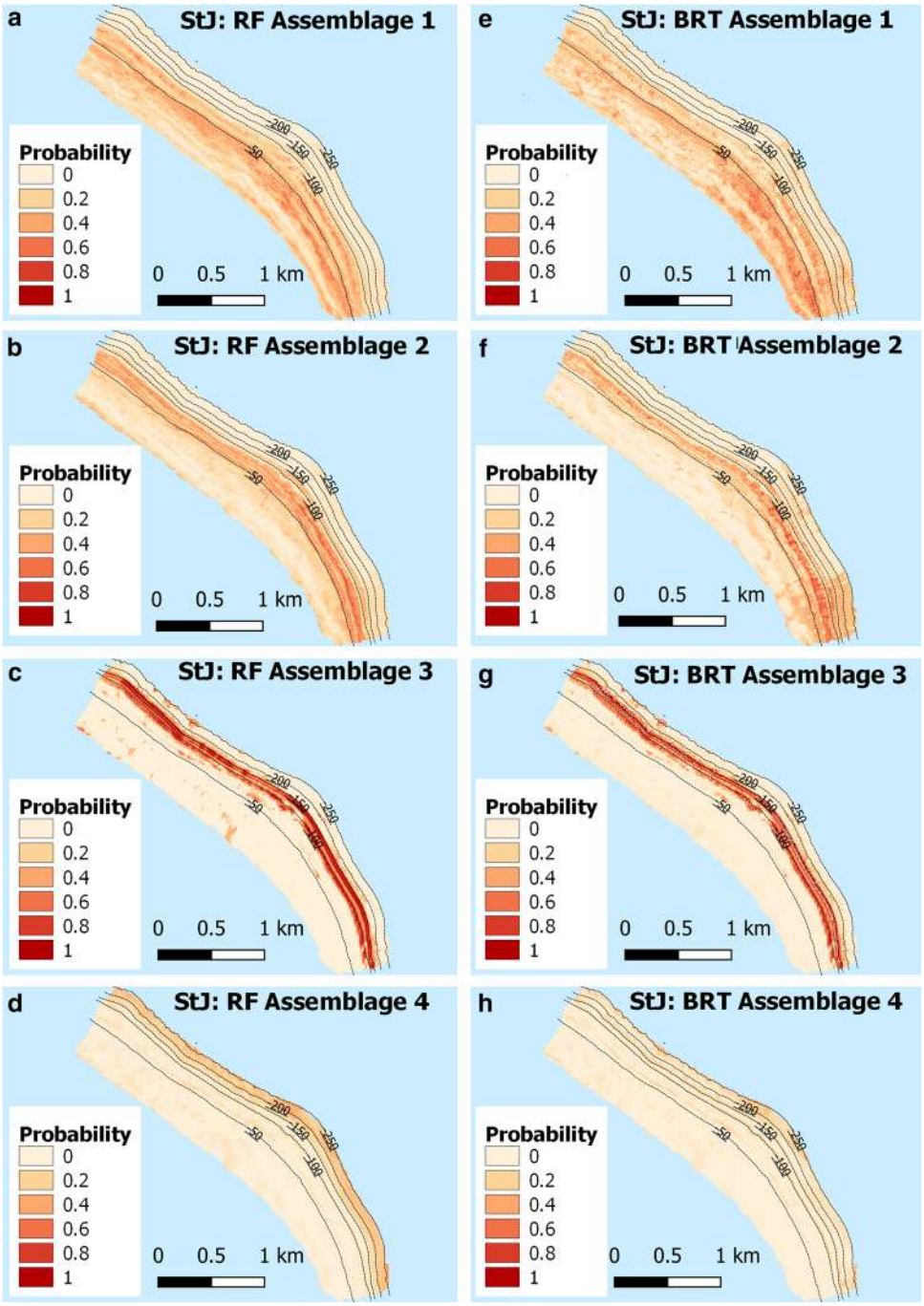


Fig. 7 Spatial predictions for deeper reef assemblages at St Joseph produced using random forests (**a**–**d**) and boosted regression trees (**e**–**h**) with depth contours at 50 m intervals. Predictive maps for other sites (Aldabra, Desroches and Poivre) are available in Online Resource 5

direct downward sediment transport (Kahng et al. 2010). In this context, locally elevated features, measured by terrain curvature, might prevent communities being covered by sediment falls (Sherman et al. 2019). Assemblage 4 was found beyond 200 m depth, but it proved challenging to define habitat conditions. Megabenthos characterizing these assemblages occur on patches of hard substrate interspersed among soft substrate, and the resolution at which spatial predictors were extracted likely did not capture substrate variation at this fine scale. Additionally, limited observations of this assemblage were available.

Vertical connectivity between shallow and deeper reefs has been an important focus of recent studies and is essential to assess the potential refugia and reseeding function of MCEs (Holstein et al. 2016). With statistically distinct assemblages, this study provides evidence of limited vertical connectivity between the surveyed deeper reefs. However, the nMDS plots and habitat suitability maps revealed that

the mesophotic assemblages (30 m, 60 m and 120 m) had some overlap and were distinct from rariphotic systems. These overlaps are driven to some extent by depth-generalist species found across multiple depths (Table 2). The limited structural connectivity between MCEs and rariphotic reefs reflects results from other regions that MCEs are biologically unique systems (Stefanoudis et al. 2019). Further research incorporating high-taxonomic resolution data along the depth gradient is necessary for reliable inferences on actual connectivity.

Geomorphology as a proxy for WIO deeper reef occurrence

Geomorphology is a key driver of hard bottom habitat and coral reef systems across all depths (Goreau and Goreau 1973; Yesson et al. 2012). Studies focusing on the geomorphological patterns driving deeper reef occurrence have primarily been conducted in other geographies than the WIO and primarily focus on MCEs rather than rariphotic ecosystems. As our findings on drivers of rariphotic systems were less reliable, here we equally focus on MCEs. Research in US waters containing the US Caribbean, Hawaii and the Gulf of Mexico demonstrated that geomorphological structures resulting from past sea-level change around islands drive mesophotic reef colonization (Locker et al. 2010). Seascape structures including carbonate mounds (Silva and MacDonald 2017), paleo-shorelines, escarpments and terraces (Locker et al. 2010) and shelf edges (Smith et al. 2016) are of demonstrated importance for MCE habitat. Effects of relic topographic structures have also been demonstrated on the Great Barrier Reef (GBR) and Pacific, where MCE assemblages have been linked to the presence of submerged reefs (Bridge et al. 2011b, 2012) and submerged banks (Linklater et al. 2016) and the Red Sea, where submarine terraces support biodiverse MCEs (Weinstein et al. 2020). Likewise, a first study in the WIO indicates steep slopes and submarine walls may function as a priority habitat for MCEs (Osuka et al. 2021).

Our findings confirm that in the WIO, geomorphology exerts control on the occurrence and distribution of mesophotic reef assemblages. High MCE occurrence probabilities were linked to relief features at all sites that provide topographically complex habitat and hard substrates for colonization at suitable depths. This indicates that topographic structures formed through historical sea-level patterns function as a proxy of suitable topographic MCE habitat. Importantly, paleo-shorelines at 120 m depth, likely formed during the Last Glacial Maximum about 20,000 years ago (Clark and Mix, 2002), at the investigated locations were associated with high probability occurrences of assemblage 3. Submarine terraces along the insular shelf of St Joseph and Aldabra were also associated with high occurrence probabilities of assemblages 2 and 3, reflecting a second MCE proxy feature previously reported in the literature (Sherman et al. 2010; Weinstein et al. 2020). MCE assemblages occurring on shelves (30–60 m) at all sites were linked to raised relief features (Fig. 7, Online Resource 5). For example, the insular shelf at Aldabra contained elevated ridges extending along the slope, which provided hard substrate associated with higher probability occurrences of MCE habitat. The consistency between sites indicates that identified assemblage–environment relationships might hold for other coralline atolls in the region.

Methodological considerations

Due to the challenges associated with extensive sampling in environments beyond SCUBA depth, our sampling scheme was spatially limited and, because of choices made in expedition sampling strategy, depth segregated. Future surveys could use a revised protocol to provide more information on species turnover and environmental conditions between our sampling depths, for example, through transects along the depth gradient. Data collection practices influenced the quality of the predictor variables. Multibeam data were acquired on a small tender, which was sensitive to motion artefacts. These artefacts were less pronounced in 25 m- and 10 m-resolution data layers than in 2 m-resolution data layers, which, in addition to the importance of the wider terrain, may contribute to their larger variable importance. Apart from the terrain variables considered in this study, other environmental factors not captured or captured as proxies also influence habitable space. These include biological processes as competition, predation and herbivory (Kahng et al. 2010) and oceanographic parameters like water chemistry, upwelling, wave and current action. In the Indian Ocean, the monsoon regime has a strong influence on reef development and recruitment through these factors (Gischler et al. 2014). Future studies could benefit from incorporating biotic and oceanographic parameters in similar analyses.

The choice of model building and evaluation method is important as different algorithms fit different relationships and tolerance constraints between biological and environmental data. This study confirmed that random forests and boosted regression trees are suitable tools to quantify the effect of multiscale interacting environmental drivers on the occurrence and distribution of deeper reefs. However, although high model accuracy and consistent results were obtained, caution is required when these predictive maps are to be generalized for marine management applications as presented maps do not take the spatial distribution of model errors and uncertainty into account (Lecours 2017). RF and BRT spatial predictions were consistent in extent but differed in intensity. Upon visual inspection, BRT models appeared less reliable than RF models. This may be linked

to the boosting characteristic of BRTs, as the sensitivity and effect of data artefacts can be additive over many model iterations (Sexton and Laake 2007). Results for assemblage 4 also show that, despite high traditional model performance metrics, spatial autocorrelation in model residuals and the low number of observations may have underestimated model errors and resulted in erroneous relationships, such as the unreliable relationship with backscatter data. Finally, our study highlighted the importance of considering scale effects by showing that the spatial resolution at which a predictor is calculated influences model responses and variable importance.

Conservation implications

There are few specific conservation efforts targeting mesophotic and rariphotic reefs globally, yet these reefs are of value to conservation and meet the criteria to be classified as Ecologically or Biologically Significant Marine Areas (EBSAs) under the Convention on Biological Diversity (CBD) (Soares et al. 2020). Several key knowledge gaps limit evidence-based conservation and management of deeper reefs, including information on assemblage composition, drivers of occurrence and distribution and vertical connectivity (Turner et al. 2019).

Our results contribute to filling some of those knowledge gaps for deeper reef seascapes in the WIO and have been presented to Seychellois stakeholders involved in marine management and conservation. Deeper reefs are of particular interest for marine managers in Seychelles for their possible role as refuges for fish species of socio-cultural and economic value such as groupers and snappers (Tyler et al. 2009). Key takeaways from these conversations are that further application of predictive mapping approaches offers potential to maximize the information obtained from seascape structure and geographically dispersed mesophotic observations and to produce spatial predictions of suitable habitat in the WIO. Further, our results provide baseline information on the geomorphological factors that shape mesophotic reef distribution in the WIO and confirm findings from other regions and anecdotal observations that complex geomorphological structures as paleoshorelines and terraces may act as proxies for mesophotic assemblages. The consistency between the results obtained per site, despite changing geomorphologies, suggests robustness of results and is an indication that similar relationships may exist across other Seychelles' Outer Islands where detailed biological survey data may be unavailable. This is important for a large ocean nation like Seychelles where country size and funding availability limit extensive biological surveys to locate deeper reefs throughout the territory. Our findings provide a starting point for marine managers to investigate possible target locations for further studies and to assess whether these structures also form priority habitat or refuge for vulnerable or commercially important fish species within Seychelles. Establishing the importance of deeper reef habitats for these species, or a species that they feed on, is a key step towards putting these habitats under consideration for a measure of protection.

Although obtaining quantitative data of these, often remote, systems remains a critical bottleneck in informing conservation and management, as the costs of robotic tools as AUVs decrease and interest in MCEs grows we expect data on these systems to become increasingly available (Armstrong et al. 2019; Osuka et al. 2021). Combined with predictive mapping approaches, these form valuable tools to provide important baseline information assessing the character and potential distribution of unexplored MCEs.

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Author contributions DS conceptualized the study, conducted all statistical analyses and wrote the manuscript. PS and NF calibrated, analysed and annotated the benthic video data. All authors contributed to data discussions and interpretation, reviewed and provided helpful comments to the manuscript.

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

Declarations

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

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E.5 *Structure-from-Motion photogrammetry demonstrates that fine-scale seascape heterogeneity is essential in shaping mesophotic fish assemblages*

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ORIGINAL RESEARCH

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

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

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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 will 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

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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 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

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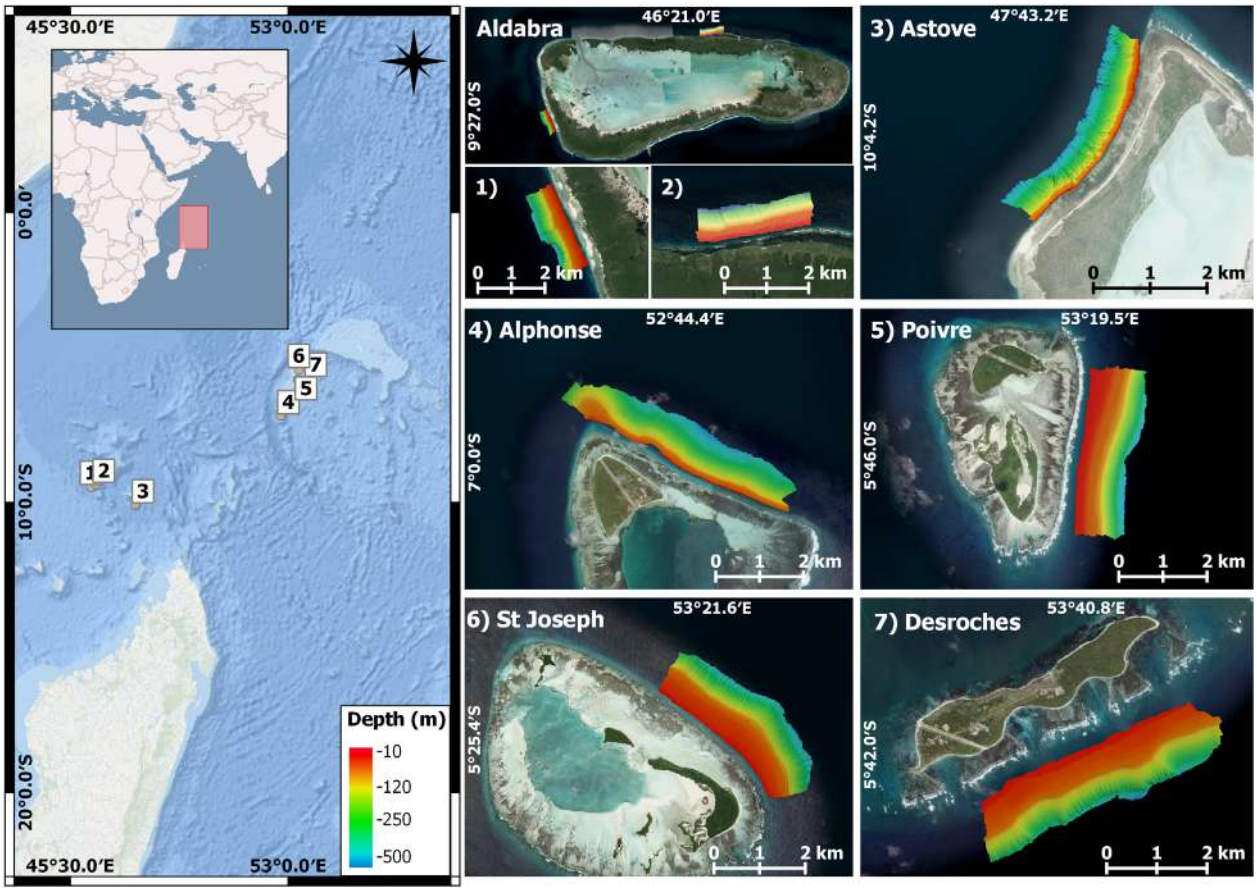


Figure 1. Map of locations surveyed during First Descent: Seychelles expedition in 2019. Swath bathymetry data collected at each site between 0 and 500 m were plotted to indicate the area in which video surveys were conducted.

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 × 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 × 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.

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

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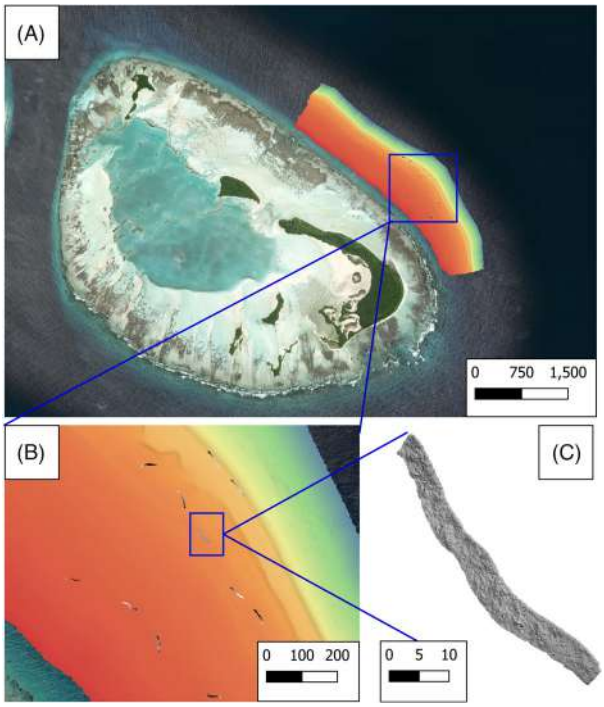


Figure 2. Example of photogrammetry transect reconstructions conducted at St Joseph. (A) shows an overview picture of the site, (B) shows transect locations at the three different depths (30, 60 and 120 m) plotted on the bathymetry, and (C) represents a close-up of a transect. The scale is in metres.

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; Samoilys 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 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

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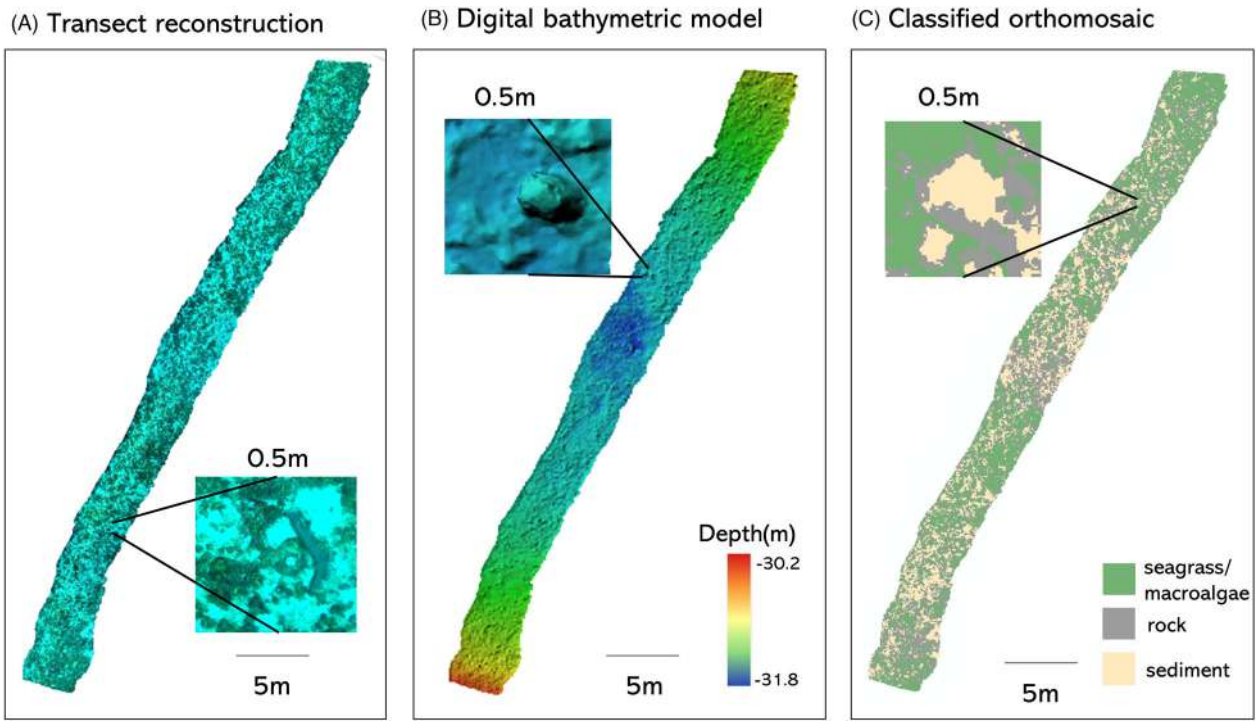


Figure 3. Outputs of benthic data extraction, demonstrated using an example from a transect at 30 m depth at Poivre. SfM photogrammetry produced a reconstruction of a transect (A), from which a digital bathymetric model (B) and an orthomosaic were exported. The orthomosaics were classified into major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

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 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

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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	Orientation of the seabed	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.

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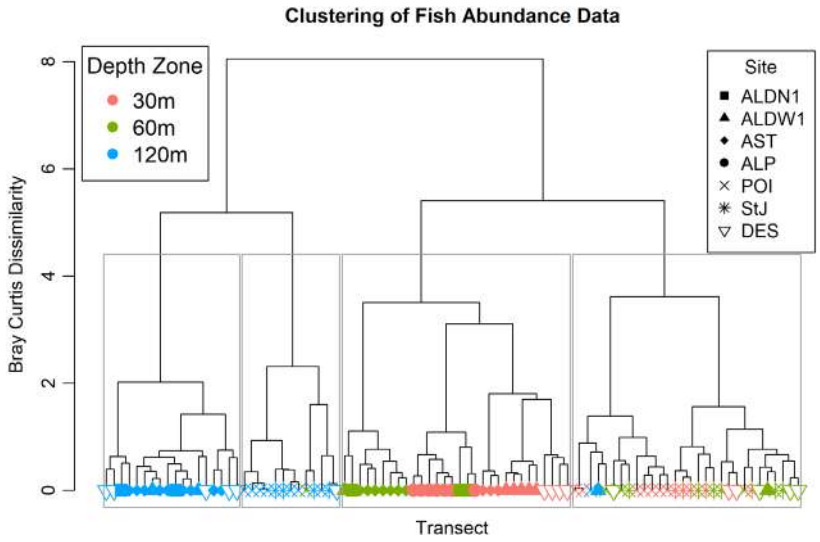


Figure 4. Clustering of fish abundance per transect where grey boxes delineate different clusters. Colours represent depth classes of observations. Symbols represent the site, with closed symbols representing off-bank islands (Aldabra, Astove and Alphonse) and open symbols representing sites on and next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

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

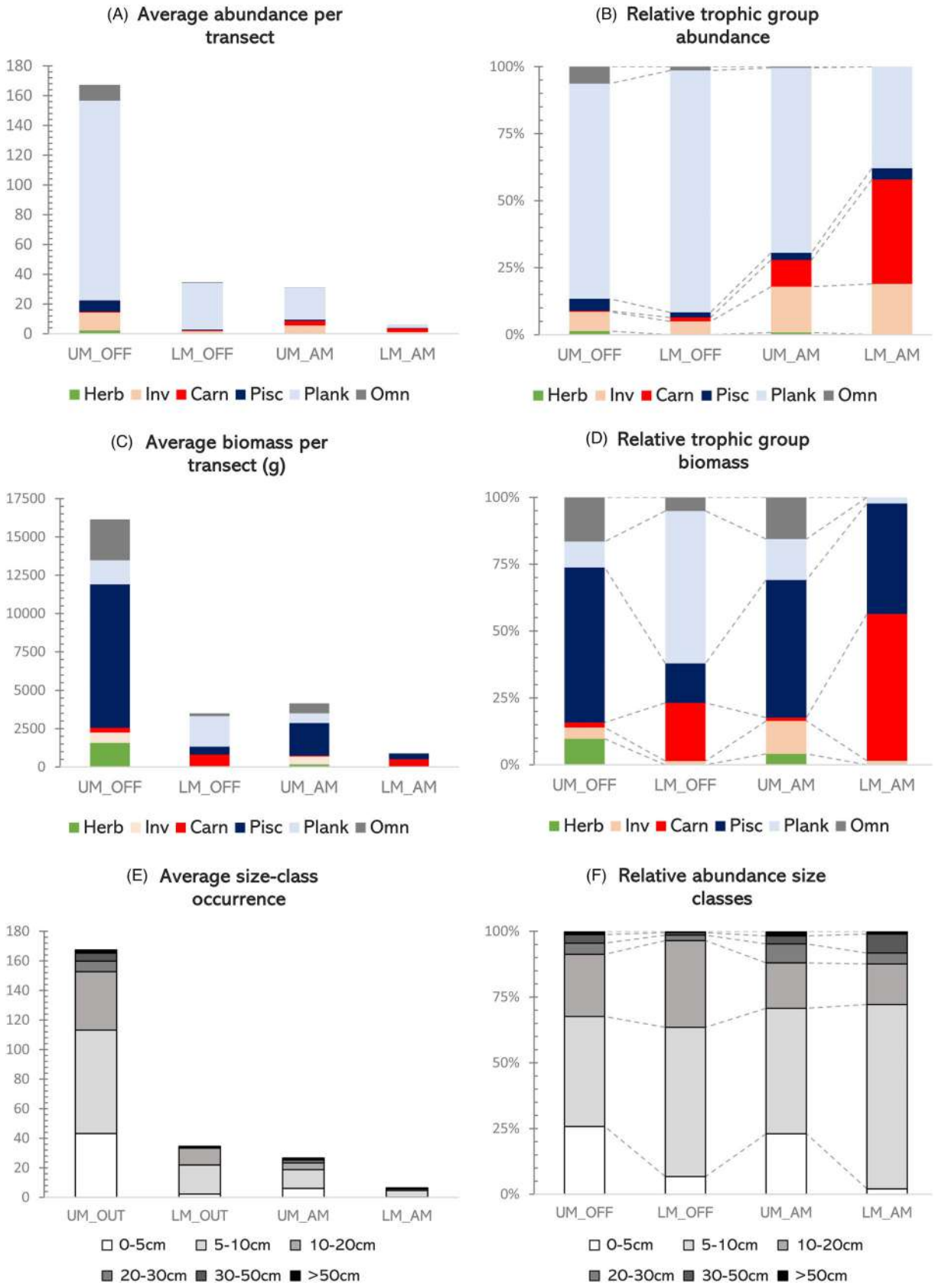
The clustering analysis on transect fish abundance and biomass data revealed four distinct depth- and site-driven groupings (Fig. 4; Appendix S3). The PERMANOVA confirmed significant differences between groupings ($P < 0.001$), and subsequent pairwise comparisons indicated that all assemblage groupings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

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

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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).

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.

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

	d.f.	Sum of squares	% total unadjusted variance explained	*P* value
(a) ANOVA abundance dbRDA				
Site*	6	8.987	24.13	<0.001
Depth*	1	5.295	14.22	<0.001
Vector Ruggedness measure*	1	1.5324	4.11	<0.001
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) ANOVA biomass dbRDA				
Site*	6	8.675	23.81	<0.001
Depth*	1	4.3784	12.02	<0.001
Vector Ruggedness measure*	1	1.5089	4.14	<0.001
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.

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, 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 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

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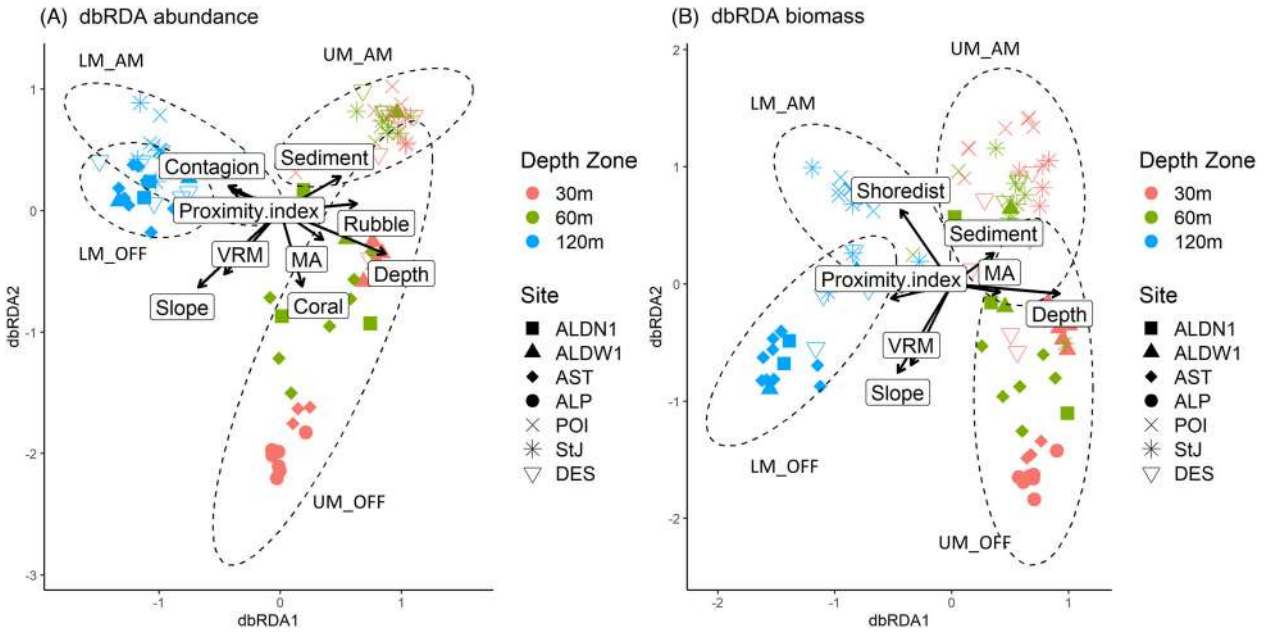


Figure 6. Ordination biplot of species abundance (A) and biomass (B) per transect as a function of dbRDA1 (17.72% variance abundance and 14.37% biomass) and dbRDA2 (10.94% variance abundance and 9.68% biomass). Point colours show the depth zones of transects, while point shapes show the site at which 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.

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 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

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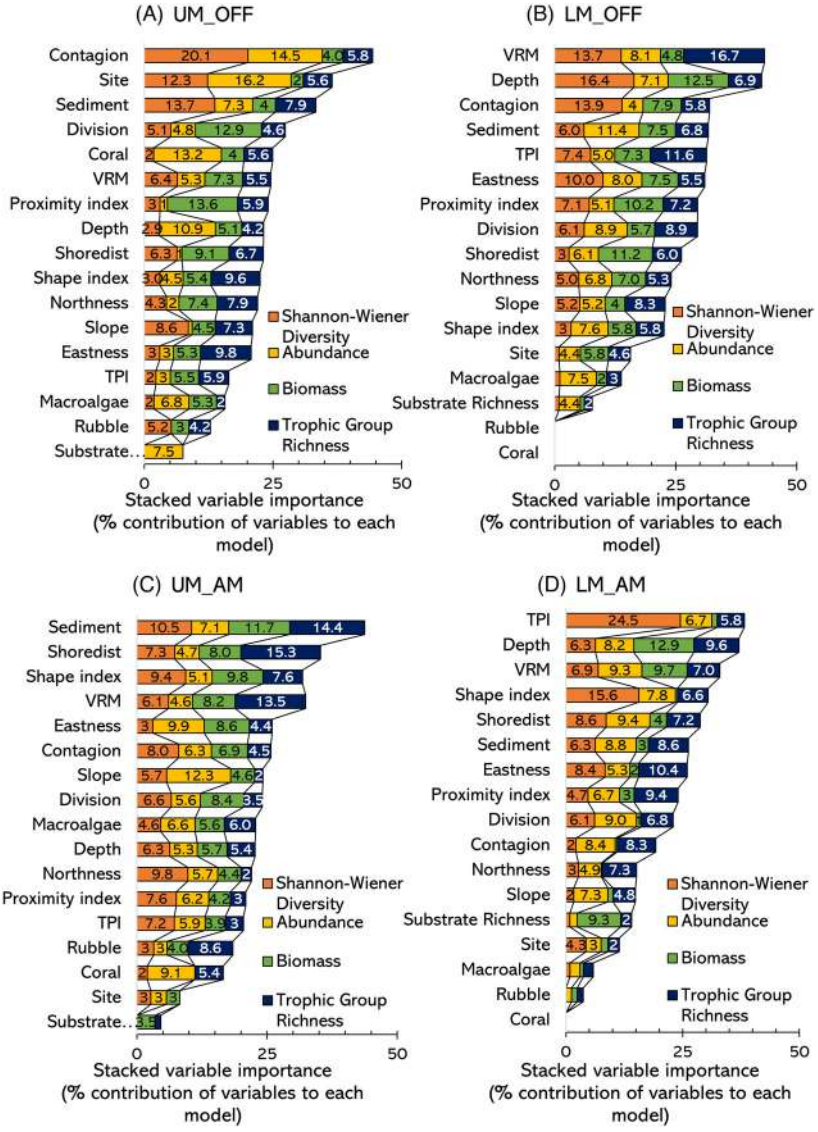


Figure 7. Variable contributions to model assemblage characteristics for the shallower assemblage of the off-bank islands (UM_OFF) (A), the deeper assemblage of the off-bank islands (LM_OFF) (B), the shallower assemblage of the Amirantes bank (UM_AM) (C) and the deeper assemblage of the Amirantes bank (LM_AM) (D). Variable contributions were standardised to a percentage of the overall assemblage descriptor model and stacked to evaluate variable importance across models.

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.

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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

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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 50mx5m 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 includec 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' Contribution

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.

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