

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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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. 2016b). 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,

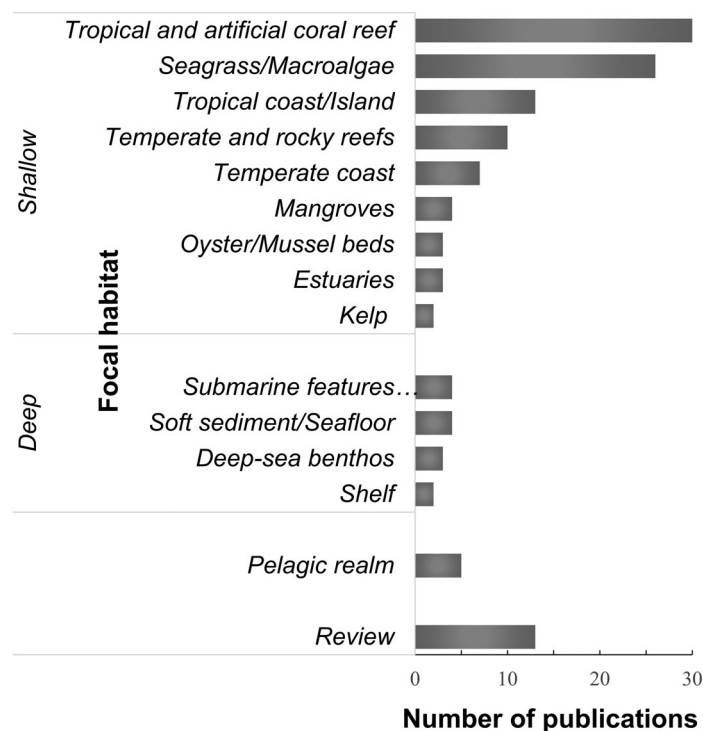


Fig. 1. Google Scholar search (1990–2021) showing peer-reviewed studies that explicitly adopt the terms “seascape ecology,” “marine landscape ecology,” or “landscape ecology” in combination with “benthic,” “seabed,” or “seafloor” and classified by focal habitat type. When shallow-water studies incorporated 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. 2016b). 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 (Hinckey 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 Geomorphic processes Sediment type and structure | Local environmental factors, flows, disturbances, geomorphic processes Transport of organic and inorganic material—erosion, sedimentation Settlement opportunities, burrowing | 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) |
| Hydrographic | Hydrodynamics/currents Water chemistry Temperature | Transport of nutrients/larvae, settlement opportunities Nutrient availability, acidification, salinity Taxa-specific thermal tolerances | Ecological connectivity (O’Leary and Roberts 2018) Importance of water chemistry and temperature in influencing octocoral habitat suitability (Yesson et al. 2012), chemical gradients around seep environments (Cordes et al. 2010) |
| 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 Tectonic activity/sedimentary disturbance regime Climate change | Structural habitat alteration Structural habitat alternation Ocean acidification, warming temperature, hypoxia, nutrient loading | Physical and biological impact of trawls on the seabed (Puig et al. 2012) Effects of sedimentological processes on benthic ecosystems (Fontanier et al. 2018) 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 (km²) 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 (Wöfl 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

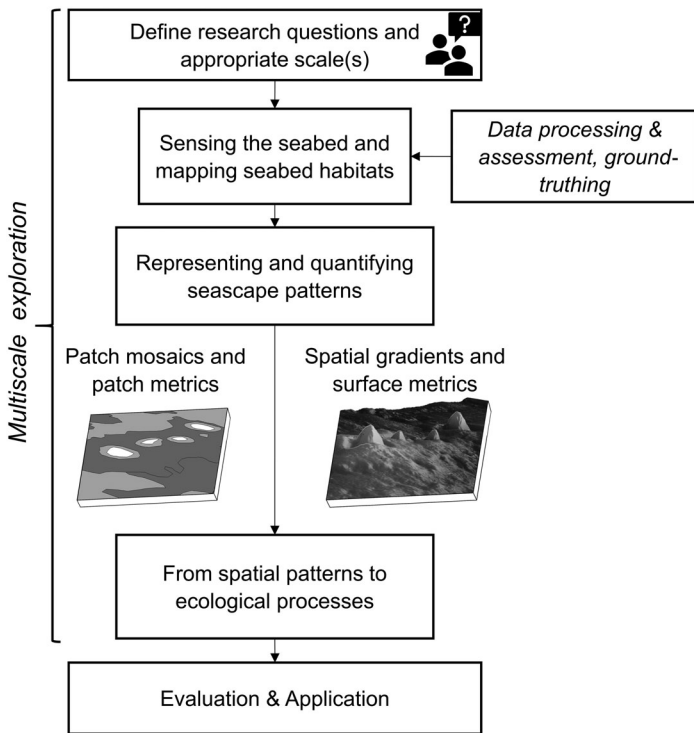


Fig. 2. Example of the logical sequence of steps in a seascape ecology approach to study benthic seascapes in the deep sea.

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. 2016a).

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 sea-floor 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

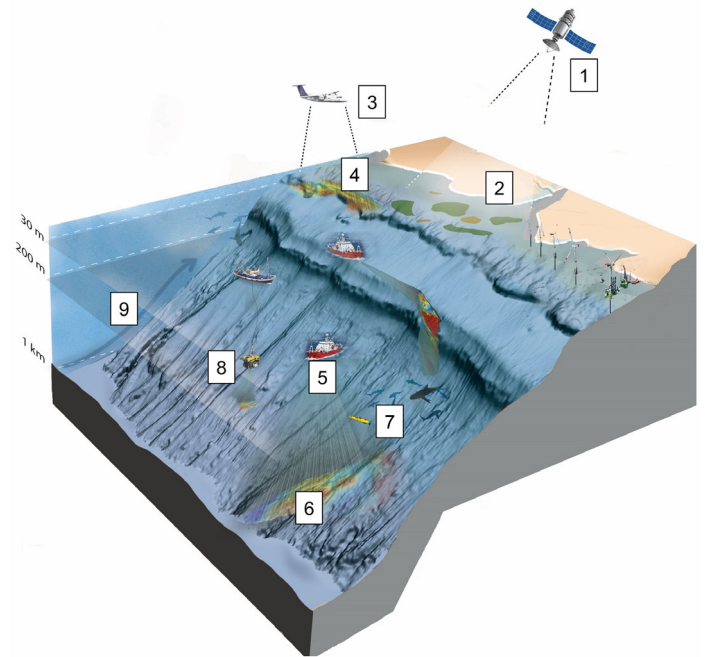


Fig. 3. A growing number of sensors, deployed both above and underwater, are available to map seabed structure. Sensors produce data with different spatial characteristics and depth limits. Satellite data (1) can be applied to map patch-based structure (2) of shallow-water environments (down to 30–50 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 ($\text{cm}^2\text{--m}^2$ 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 multi-scale 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. 2019a) (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-

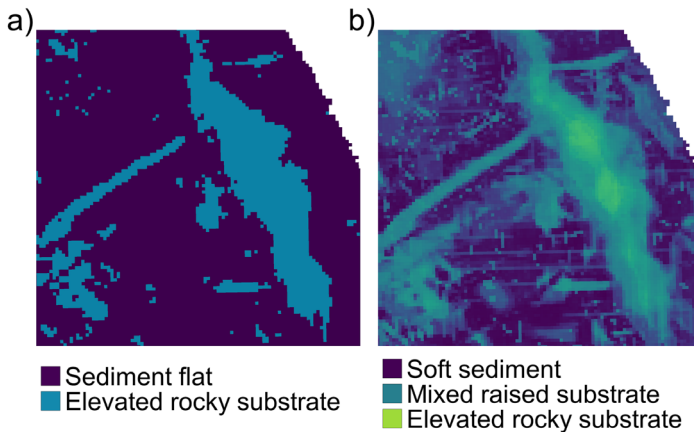


Fig. 4. Patch-mosaic (a) and continuous gradient (b) representations of seascape structure produced using bathymetry collected around Aldabra atoll, Seychelles, between 150 and 500 m depth. The patch mosaic representation homogenizes within-patch variability and enhances discrete edges, while the gradient 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. 2016b). 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 m²) 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. 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 (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. 2016a), 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. 2016b). 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) |
| | Edge to area ratio | Length of edge segments | Proxy for ecological processes through edge effects | Evaluation of structural connectivity (Proudfoot et al. 2020) |
| 2D—configuration | 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 | |
| 2.5D—terrain structure | Fragmentation index | A measure of landscape splitting in discrete patches | Disturbance to habitat 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 | Species–habitat associations and distribution of demersal fish (Borland et al. 2021) |
| Habitat complexity (e.g., rugosity, vector ruggedness measure) | Critical for ecological functions and habitat prediction | Settlement opportunities, microhabitats, shelter from exposure | Determining hotspots of predator activity (Bouchet et al. 2015) | |

(Continues)

Table 3. Continued

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

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 multi-dimensional configuration of the seascape, has been the focus of seascape ecology efforts to quantitatively link seascape heterogeneity to biological distribution patterns, organism

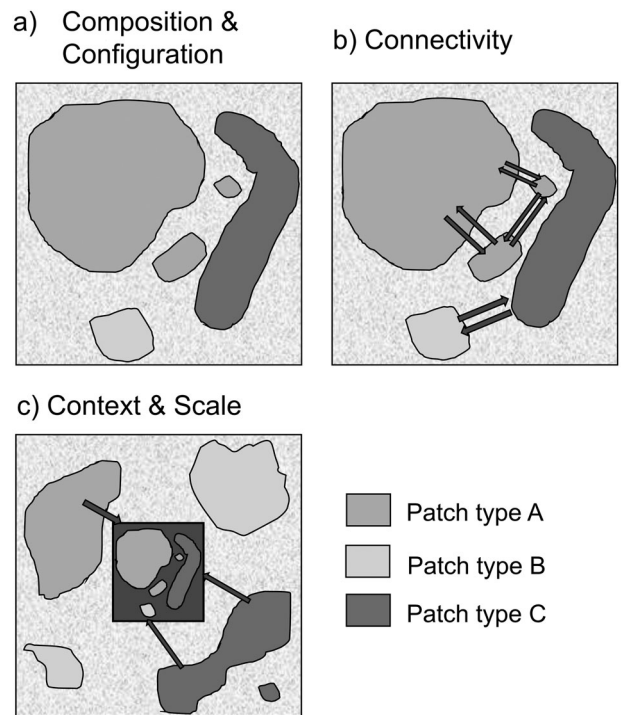


Fig. 5. Schematic representation of patch-based seascape structure at the seabed, based on the patch-matrix model. Seascapes differ in the composition and configuration of habitats (a), such as their size and shape, which influences processes as connectivity in the seascape (b). The surrounding environment (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 interspersed 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. 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. 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 (Tremblay 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. 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 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, benthic-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. 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. 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

None declared.

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