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PERSPECTIVE

Deep ocean seascape ecology: gaps and pathways for application

Denise J. B. Swanborn · E. Simon-Lledó · E. A. Thomas · T. Bond · C. R. McClain · A. Metaxas · G. M. Nester · Y. Niyazi · G. Bribiesca-Contreras · M. Clavel-Henry · A. Marchiò · J. Montenegro · A. J. Jamieson

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Abstract
Context The ecological implications of multi-scale spatial heterogeneity remain poorly resolved in many parts of the ocean, especially at abyssal (3000–6000 m) and hadal (> 6000 m) depths. Seascape ecology offers a framework to link spatial patterns with ecological processes but remains an emerging approach for biodiversity research in the deep sea.
Objectives We aim to promote wider recognition of seascape ecology as a unifying framework for understanding biodiversity, spatial patterns, and processes across scales in the deep ocean. Specifically, we aim to identify strategic priorities to advance seascape ecology in abyssal and hadal environments and to transform the framework from concept to practice.
Methods We adapt foundational concepts of seascape ecology—Composition, Configuration, Connectivity, and Context —to deep-sea ecosystems across multiple scales. For each, we assess current knowledge, highlight key research gaps, and propose practical avenues for future application.
Results & Conclusions Research gaps and priorities are outlined for each concept, as well as an operational workflow. Cross-cutting needs include multi-scale sampling and analysis, integration of abiotic and biotic data, incorporation of traits and phylogeny, improved temporal coverage, and greater technological and methodological standardisation.

Keywords Deep sea · Abyssal zone · Hadal zone · Environmental heterogeneity · Biodiversity patterns · Marine biogeography · Connectivity · Scale dependence

D. J. B. Swanborn (✉) · E. A. Thomas · T. Bond · G. M. Nester · Y. Niyazi · A. Marchiò · J. Montenegro · A. J. Jamieson
Minderoo-UWA Deep-Sea Research Centre, School of Biological Sciences and Oceans Institute, The University of Western Australia, Perth, WA, Australia
e-mail: denise.swanborn@uwa.edu.au

E. Simon-Lledó
Institut de Ciències del Mar (ICM-CSIC), Pg. Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

C. R. McClain
Department of Biology, University of Louisiana at Lafayette, Lafayette, LA, USA

A. Metaxas
Department of Oceanography, Dalhousie University, Halifax, NS, Canada

G. M. Nester
Minderoo OceanOmics Centre at UWA, Oceans Institute, The University of Western Australia, Crawley, WA, Australia

G. Bribiesca-Contreras
Marine Science, National Oceanography Centre, Southampton, UK

M. Clavel-Henry
GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Wischhofstraße 1-3, Seefischmarkt, 24148 Kiel, Germany

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Introduction

Seascape ecology emerged from landscape ecology as a multidisciplinary framework to understand how spatial heterogeneity influences ecological patterns, processes, and connectivity in marine systems (Boström et al. 2011; Wedding et al. 2011; Pittman et al. 2021; Swanborn et al. 2022b). The field examines the dynamic interplay between structure and function across multiple spatial and temporal scales, linking biodiversity, ecosystem functioning, and biological change (Steele 1989; Levin 1992; Pittman 2017). Extending landscape-based concepts to marine systems, seascape ecology helps understand the ecological implications of environmental heterogeneity and supports ecosystem-based ocean stewardship (Wedding et al. 2011; Pittman et al. 2021; Swanborn et al. 2022b). Despite advances in geospatial technologies, sensors and analytical techniques (Danovaro et al. 2020; Aguzzi et al. 2024), these principles have not been widely applied to marine biodiversity research, especially in the deep sea.

The deep sea comprises the largest biome on Earth, extending from continental margins across abyssal plains into deep trenches (Ramirez-Llodra 2020). Challenging long-held paradigms in ecology (Smith and Snelgrove 2002), deep seascapes are vast, highly diverse, and nutrient-poor (Smith et al. 2008; Ramirez-Llodra et al. 2010), and provide vital services, such as nutrient cycling (Arrigo 2005; Middelburg 2018) and supporting benthopelagic food webs (Iken et al. 2001; Drazen and Sutton 2017). These environments can be conceptualised as spatially complex, three-dimensional "seascapes" in which multiscale environmental gradients structure mosaics of habitats and communities. At basin scales, abyssal plains are punctuated by ridges, seamounts, and fracture zones, and characterized by variations in surface sediment composition (Harrison et al. 2025), while trenches introduce large vertical gradients in pressure, topographic complexity, bottom water properties, and oceanographic conditions (Fig. 1) (Clark et al. 2010; Ramirez-Llodra et al. 2010; Stewart and Jamieson 2018; Kolbusz et al. 2024). Substratum type, sediment characteristics, and microtopography

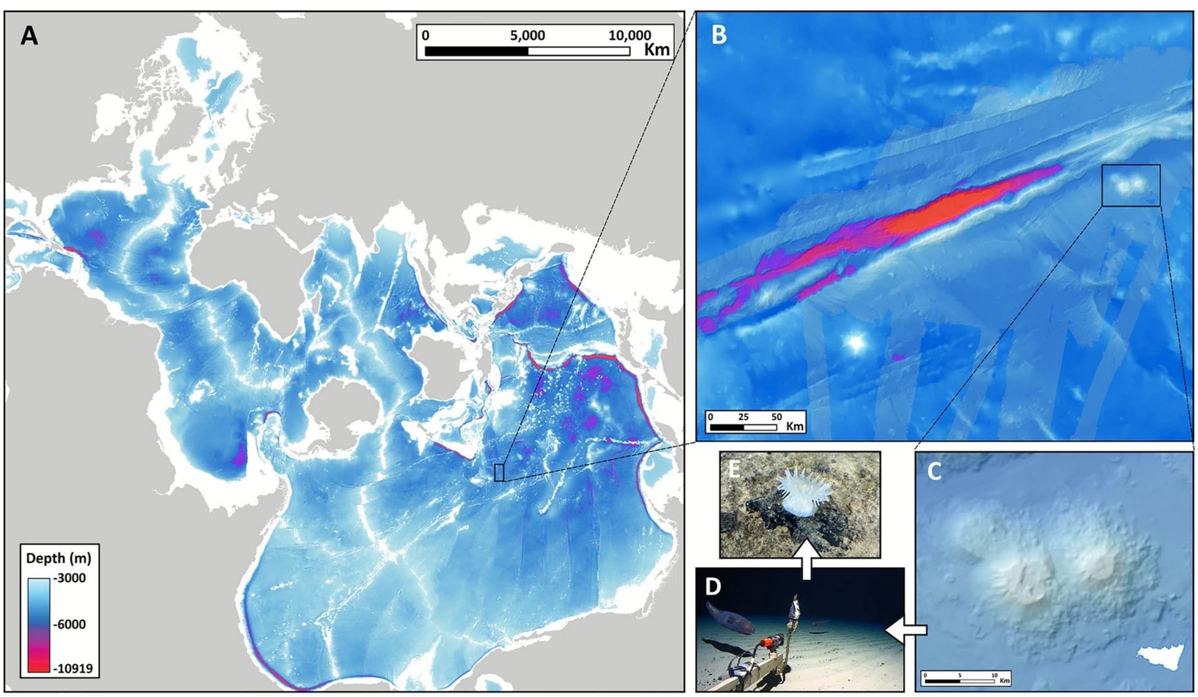

Fig. 1 Spillhaus square projection map of the world ocean for the seafloor showing the abyssal and hadal depth zones (**A**). Bathymetry data from the Global Bathymetric Chart of the Oceans (GEBCO Compilation Group 2024). Insets show seascape structure across mega- (**B**), meso- (**C**), macro- (**D**) and micro- (**E**) scales using data collected in the Nova Canton Trough during the Inkfish Open Ocean Program Nova Canton Trough expedition (Jamieson et al. 2024)

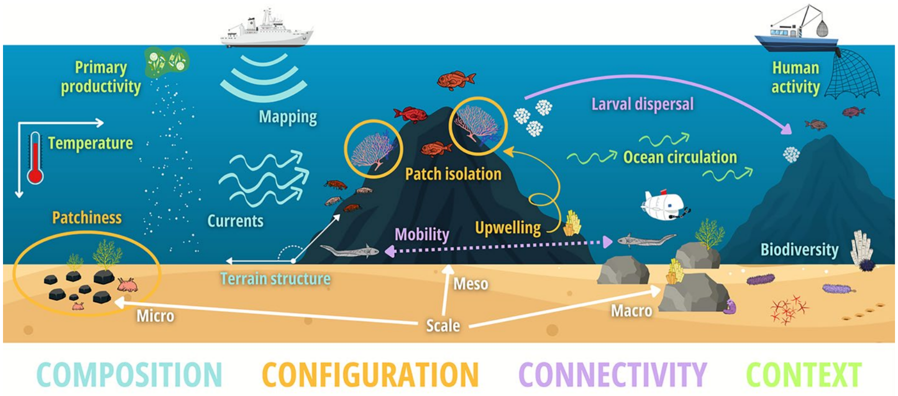

Fig. 2 Schematic representation of the four Cs of seascape ecology and their application to deep-sea environments across micro- to meso-scales. Colours used are representative of each concept

shape seafloor heterogeneity within these features at finer spatial scales (Grassle 1989; Etter and Grassle 1992; Levin et al. 2001; Ramirez-Llodra et al. 2010; Durden et al. 2015), while overlying oceanographic processes, including current regimes, water mass and chemical boundaries, circulation patterns, the location of the oxygen minimum zone (OMZ), and critically, the supply of particulate organic matter (POM) from the surface, govern energy flow and benthic conditions (Lutz et al. 2007; Smith et al. 2008; Yasuhara and Danovaro 2016; McClain et al. 2020; Simon-Lledó et al. 2023a). Episodic events such as food pulses, seismic activity or benthic storms introduce temporal variability (Gooday 2002; Gardner et al. 2017).

Understanding environmental heterogeneity across horizontal and vertical gradients, and how biodiversity responds to environmental mosaics, is central to marine ecology, particularly in the deep sea. Spatial variation underpins species occurrence and distribution, connectivity, ecological function, and resilience in the face of both natural and anthropogenic disturbances (Levin et al. 2001). Despite the high diversity of ecosystems in the deep sea and their ecological significance, our ability to study the ecological implications of environmental heterogeneity remains limited, partly due to the persistent data scarcity (though this challenge is not unique to deep-sea environments, see Hortal et al. 2015) but also a lack of unified analytical frameworks that explicitly integrate environmental heterogeneity across scales.

Seascape ecology provides a spatially explicit framework for understanding how environmental heterogeneity, combining continuous gradients and patchiness, influences biodiversity, ecological patterns, and associated processes (Turner and Gardner 2015; Pittman 2017). The conceptual framework is organised around several key Cs (Pittman et al. 2021; Swanborn et al. 2022b). Here, we explicitly add Composition to the original four Cs defined by Pittman et al. (2021), reflecting challenges around resolving the elements that form seascape structure in deep-sea environments. The research themes are: Composition (the environmental and biological seascape elements – species and habitats – that are present), Configuration (the arrangement of seascape elements), Connectivity (how these elements are linked across space) and Context (broader environmental drivers that shape the system under consideration) (Fig. 2). Importantly, the application of these Cs requires explicit Consideration of scale (Fig. 1), with spatial and temporal scale shaping both the detection of patterns and the derived interpretation (Wiens 1989; Levin 1992). Seascape units can be delineated at different scales, depending on the phenomenon under consideration (Table 1).

Although many deep-sea studies implicitly apply these concepts (Levin et al. 2001; Smith et al. 2008; Cordes et al. 2010; McClain et al. 2020; Jamieson et al. 2021; Simon-Lledó et al. 2023a), they are rarely integrated or operationalised under a cohesive framework. We aim to present the Cs of seascape ecology as a conceptual framework to improve the study of biodiversity-environment relationships in benthic deep-sea environments, with emphasis on abyssal (3000–6000 m) and hadal systems (> 6000 m) (Fig. 1). While pelagic environments are a critical component of the seascape (Sutton et al. 2017; Haddock and Choy 2024), and could be conceptually studied using the Cs framework, we

Table 1 Conceptual position of seascape ecology relative to other disciplines

Concept / Approach	Core focus	Distinguishing characteristics and relevance
Landscape/Seascape ecology	Relationship between spatial patterns and ecological processes across space and time	Integrates pattern, process, and scale; emphasises how landscape structure (composition and configuration) influences ecological flows, species interactions, and ecosystem function
Macroecology	Broad-scale patterns of abundance, distribution and diversity	The study of broad-scale patterns and processes in biodiversity, abundance, and distribution of organisms across large spatial and temporal scales
Biogeography	Distribution of life and biological patterns across space and time	Describes and explains how species, communities and ecosystems are arranged geographically and temporally. Focuses on where biodiversity occurs and the historical and evolutionary processes shaping these patterns, rather than the mechanistic role of spatial structure per se
Conservation biogeography	Application of biogeographic principles to biodiversity conservation	Applies biogeographic theory to conservation planning by linking species distribution patterns with management and policy. Guides the delineation of biogeographic units and prioritisation frameworks such as EBSAs and MPA networks
Ecosystem ecology	Flow of energy and materials through interacting biotic and abiotic components of ecosystems	Examines the flow of energy, materials and nutrients between organisms and their environment, emphasising the processes and feedbacks that maintain ecosystem function rather than the dynamics of individual species
Community ecology	Structure and dynamics of assemblages of interacting species	Focuses on how multiple species living in the same environment interact through processes such as competition, predation, and facilitation, and how these interactions influence biodiversity patterns and ecosystem structure
Population ecology	Demography and dispersal of species	Studies the dynamics of a single taxon through time and across environments, focusing on the demographic and environmental processes that regulate abundance, distribution, and persistence
Landscape/seascape genomics	Spatial genetic structure in relation to environmental heterogeneity	Examines how environmental heterogeneity influences gene flow, connectivity, adaptation, and population structure, integrating genome-wide molecular data with environmental and spatial analyses to identify adaptive loci and evolutionary drivers

deliberately focus on the benthos, where the opportunity to apply fundamental seascape theory principles is currently greatest. We translate the conceptual underpinnings of seascape ecology to deep-sea ecosystems, and for each of the Cs, identify key research gaps and outline practical avenues for their application in future deep-sea research (Figs. 2 and 3). By doing so, we seek to promote wider recognition of seascape ecology as a common framework for understanding biodiversity, spatial patterns and processes across scales in the deep ocean.

Composition: what is there? Recommendations for mapping environments, habitats and biodiversity

Understanding the *composition* of a deep seascape (the occurrence and distribution of its environmental features, habitats and biological communities) is foundational for interpreting biodiversity patterns and ecosystem processes. Composition encompasses both abiotic (bathymetry, substrate type, water mass properties, food supply) and biotic (species, traits, abundance, biomass, genetic variation) elements that make up seascapes (Fig. 2, Table 2). Composition forms the basis from which configuration, connectivity and context can be understood.

Abiotic characterisation

Seafloor geomorphology, substratum type and overlying oceanography are key abiotic factors shaping composition. Bathymetry and terrain types delineate megahabitats (e.g., abyssal plains, trenches, fracture zones) that structure deep-sea biodiversity (Fig. 1). Multibeam echo sounders (MBES) provide the primary source (> 95%) of bathymetric data at abyssal and hadal depths, typically resolving features at ~10–100 m resolution (Niyazi et al. 2025), while global compilations of seafloor topography, such as GEBCO (Mayer et al. 2018) and GMRT (Ryan et al. 2009) capture broad-scale features, but remain coarse. High-resolution mapping, particularly using remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) equipped with MBES and side-scan sonars (SSSs), captures environmental characteristics in finer-scale (10's cm-m) resolution (e.g., Wynn et al. 2014; Huvenne et al. 2018).

Oceanographic variables (temperature, salinity, oxygen, currents, nutrients, plankton, chlorophyll, etc.) are collected through a combination of ship-based measurements, autonomous platforms (e.g., AUVs, Argo floats, gliders), long-term moorings and buoys, and satellite observations (e.g., Lin and Yang 2020) and integrated through programs and repositories like the Global Ocean Ship-Based Hydrographic Investigations Program (GO-SHIP), World Ocean Atlas (https://www.ncei.noaa.gov/products/world-ocean-database), Copernicus Marine Environment Monitoring Service (CMEMS, https://marine.copernicus.eu/) and Bio-ORACLE (https://bio-oracle.org).

Table 2 Multi-scale compositional heterogeneity in deep-sea seascapes (scale following Greene et al. 2007)

Scale	Example feature	Abiotic drivers	Biotic expression	Survey methods/data sources
Mega (> 1 km) (Fig. 1b)	Abyssal plain, basin, subduction trench, fracture zone, Submarine canyon, seamount	Biogeographic diversity: basin-scale geomorphology, water mass structure, productivity regime	Biogeographic provinces, regional species pools, compositional turnover, broad depth zonation, ecological connectivity	GEBCO (2025), GMRT (Ryan et al. 2009), World Ocean Atlas (Mishonov et al. 2024), OBIS records
Meso (10 s m –1 km) (Fig. 1c, Fig. 2)	Top/flank of seamount, submarine canyon head, reefs, extensive bedrock outcrops, nodule fields, hydrothermal vent fields	Geomorphological complexity: regional topography, slope, orientation, internal tides	Ecological assemblages, depth zonation, ecological corridors for dispersal	Shipborne MBES/backscatter, regional biogeochemical surveys
Macro (1 m-10 m) (Fig. 1d, Fig. 2)	Seafloor bedforms, rafted blocks, pockmarks, bedrock outcrops	Structural complexity: local topography, substrate type assemblages, current regimes, sedimentation, organic matter input and distribution	Distinct assemblages across features, assemblage and beta-diversity turnover, trait-specific filtering, edge effects	Ultra-high-resolution MBES, AUV/ROV mapping, stereoimaging, water sampling trawls, imagery surveys
Micro (cm-1 m) (Fig. 1e, Fig. 2)	Boulders, gravels, dropstones, biogenic habitats, individual nodules	Substrate diversity, substrate patchiness, microtopography, bioturbation, *lebensspuren*	Colonisation, localised richness, local coexistence	In-situ imagery, sediment cores, SfM photogrammetry

While these have greatly advanced our ability to characterise oceanographic conditions, they often lack the resolution and precision below 3000 m required to resolve abyssal and hadal benthic boundary layers and conditions that drive biodiversity. Likewise, analytical challenges remain in separating the pervasive influence of depth from correlated water-mass properties: temperature, oxygen, and salinity covary with depth, but can exert independent effects on species occurrence.

Biotic characterisation

Information on biotic elements of composition in the deep sea has historically relied on trawls, cores and, more recently, in-situ imaging. While effective, these methods are often spatially patchy (Bridges and Howell 2025), or in the case of imaging, taxonomically incomplete. Taxonomic precision varies across taxonomic groups and imaging methods. Open Nomenclature (ON) symbols to indicate standardised levels of identification are increasingly used to enhance the clarity, precision, and comparability of image-based biodiversity data (Horton et al. 2021, 2025), substantially increasing the accuracy of combined image-based and molecular taxonomic characterisation (Kersken et al. 2019; Bribiesca-Contreras et al. 2022; Stratmann et al. 2025). Such integrative taxonomy provides the baseline for emerging approaches, such as metabarcoding and environmental DNA (eDNA), to detect species presence, faunal turnover, and seascape boundaries, including at abyssal and hadal depths (Djurhuus et al. 2020; Laroche et al. 2020; Verhaegen et al. 2025). Importantly, biotic composition extends beyond species lists to also include genetic and functional variation, abundance, biomass, and/or energy, all of which underpin ecosystem functioning and ecological processes.

Seascape representation

From a seascape perspective, composition can be represented using patches, mosaics or gradients (Fig. 2). At the broadest scale, biogeographic classification schemes integrate oceanographic properties with biological distributions to delineate deep-sea provinces, from Vinogradova (1979, 1997) and Belyaev's (1989) early iterations to modern reassessments (Briones et al. 2009; Watling et al. 2013; Simon-Lledó et al. 2023a). At finer scales, spatially continuous environmental datasets and biological data provide inputs to habitat classification approaches, theoretically delineating ecologically meaningful units and generating seascape maps (McQuaid et al. 2020; Misiuk and Brown 2024). Bathymetric terrain models underpin habitat characterisation, either using a patch-based model (Wedding et al. 2011), continuous gradients in environmental conditions (McGarigal and Cushman 2005; Lepczyk et al. 2021) or a combination of both patch and gradient models. Hierarchical frameworks (Wu and Loucks 1995; Greene et al. 1999; Aguzzi et al. 2020) are especially relevant, capturing compositional variation at nested scales (Table 2).

Patch-matrix and patch-mosaic models conceptualise seascapes as discrete units embedded in a wider matrix, or as dynamic mosaics differing in size, shape and persistence (Forman and Godron 1981; Lausch et al. 2015). Recognition of the benthos as a heterogeneous mosaic (Frederick Grassle and Sanders 1973; Grassle 1977) overturned the once-dominant view of the abyss as a featureless and homogeneous plain, and paved the way for contemporary seascape approaches in the deep sea. Metrics such as patch size and diversity (Table 3) quantify compositional heterogeneity (Cushman et al. 2008; Wedding et al. 2011) while continuous gradients can be characterised through topographic variables or species distribution models (e.g., Uhlenkott et al. 2022).

Composition is expressed differently across scales (Fig. 2). Trenches can be viewed as distinct megahabitat patches within the wider abyssal matrix, where abrupt depth breaks and horizontal isolation create barriers (Fig. 1, Table 2), often resulting in high species endemism within a trench, or across neighbouring trenches (Jamieson and Weston 2023). At mesoscales, variation in environmental parameters such as depth, current regime, oxygen concentrations, and substrate type influences the distribution, abundance, and diversity of fauna, leading to flank-specific assemblages and vertical zonation (Kennedy et al. 2025). At microscales, small and isolated patches, such as rocky areas and nodules (Fig. 1e, Mejía-Saenz et al. 2023), dropstones (Meyer et al. 2016), or biogenic features from small sponge stalks (Beaulieu

Table 3 2D Metrics of composition and configuration (Turner and Gardner 2015), and examples from deep-sea environments

Metric type	Definition	Common metrics	Deep-sea example	Ecological implication
Patch area	Area of discrete seascape unit	% cover, mean patch size, largest patch index	Extent of a sponge ground	Larger patches support higher species richness and abundance; less prone to local extinction
Patch diversity	Diversity of patch types	Shannon diversity, richness	Range of substratum types in a feature	Higher patch diversity increases potential species and functional diversity
Patch shape and edge	Shape of habitat patch, length of edges	Shape index, fractal dimension, edge density	Biozonation in hydrothermal vents	Edge effect; gradient effects; ecotones vs ecoclines
Patch isolation	Distance between habitat patches	Nearest-neighbour distance, Euclidean distance, proximity index	Separation between vent fields or trenches	Determines dispersal success and connectivity, affects recolonisation and extinction risk
Patch arrangement	Ordering or spatial sequencing of patch types	Contagion index, adjacency metrics	Sequential ordering of habitat types in a feature	Determines directional dispersal pathways and ecological gradients; enhances stepping-stone processes across depth and topography
Patch clustering	Degree to which patches are aggregated or dispersed	Clumpiness index, aggregation index	Clustering of nodules within a nodule field	High clustering facilitates faunal exchange and local connectivity; dispersed patches may limit dispersal and increase isolation effects

2001) to large whale falls (Smith et al. 2015), can modulate the abundance and diversity of fauna and their community structure by creating fine-scale habitat heterogeneity.

Key gaps

Despite global mapping and biological initiatives (Table 4) several critical gaps remain:

1. *Resolution and spatial coverage mismatch:* Global bathymetric, biogeochemical or oceanographic datasets remain too coarse to resolve ecologically relevant benthic heterogeneity at abyssal and hadal depths, while high-resolution terrain models, knowledge on benthic water-mass properties and biological data are spatially restricted. This mismatch means that biodiversity-environment relationships are often studied at a single scale, depending on data availability, and rely on proxies.
2. *Distribution of geographic and depth data:* Observations are geographically biased towards certain research tools, geographic regions of specific interest (e.g., the Clarion-Clipperton Zone) or clustered towards more accessible features and depths (Bridges and Howell 2025), limiting knowledge about the geographic distribution of species (Wallacean shortfall; Hortal et al. 2015) and their responses to abiotic conditions (Hutchinsonian shortfall; Cardoso et al. 2011; Hortal et al. 2015).
3. *Taxonomic impediment:* While species are the fundamental units of biodiversity, many deep-sea species or groups remain undescribed owing to limited time and resources, and dwindling taxonomic expertise (Rabone et al. 2023; Rogers et al. 2023; Hutchings et al. 2025) (Linnean shortfall). Consequently, published datasets often use informal names, making them incomparable in the absence of genetic data (e.g., Washburn et al. 2021). Environmental DNA is increasingly

Table 4 Relevant existing international initiatives for addressing gaps in the application of core seascape ecology concepts

Gap	Relevant initiative(s)	How it helps
Limited high (multi)-resolution global bathymetry	Seabed 2030, Global Multi-Resolution Topography (GMRT)	Provides global bathymetric coverage with multiple resolutions; integrates national and regional datasets
Availability of global species and trait records	OBIS and World Register of Marine Species/World Register of Deep-Sea Species (WoRMS/WoRDSS)	Aggregates biodiversity data, integrates taxonomic standards
Integration of biodiversity with environmental variables, data interoperability	Global Open Ocean and Deep Sea (GOODS), Global Ocean Observing System (GOOS), Deep-Ocean Observing Strategy (DOOS)	Sustained ocean observations, identifying Essential Ocean variables (EOVs) and Essential Biodiversity Variables (EBVs) monitor for deep-sea ecosystems, global biogeographic classification
Temporal coverage of biodiversity observations	European Multidisciplinary Seafloor and Water Column Observatory (EMSO), OceanSITES, Ocean Networks Canada (ONC), Deep Argo	Provides long-term, high-frequency oceanographic and ecological observations to capture temporal variability
Global capacity	Challenger 150, African Network of Deep-Water Researchers, Ocean Voices, Ocean Discovery League (ODL), Crustal Ocean Biosphere Research Accelerator (COBRA)	Improved capacity to undertake offshore and deep-sea research, improved engagement of marine scientists from varied backgrounds, and development of low-cost technology to access deep-sea environments
Coordination of deep-sea research to address known data gaps	Ocean Census, Challenger 150, Senckenberg Ocean Species Alliance (SOSA)	Promotes collaboration initiatives to accelerate deep-sea exploration and species discovery
Scarcity of trait-based data	sFDvent	Provides a global functional traits database for vent fauna, serving as a model for extending trait-based frameworks to other deep-sea habitats
Application of results derived from seascape approaches	Deep-Ocean Stewardship Initiative (DOSI), Ocean Voices	Integrates science into policy processes related to the deep ocean to advise on ecosystem-based management and maintain the integrity of deep-sea ecosystems

applied at abyssal depths (Laroche et al. 2020; Iguchi et al. 2024) and is emerging in hadal environments (Rivera Rosas et al. 2024), but it is hindered by incomplete reference libraries (Horton et al. 2025).

4. *Data interoperability:* Imaging, sampling and sequencing generate heterogeneous deep-sea biodiversity datasets. Advances in sequencing technology and the use of video or photographic surveys have dramatically increased our ability to understand seascape composition, but have resulted in a multitude of informal names with few formal comparisons across scales. Consequently, datasets are often incomparable, community assessments are frequently coarse and reliant on morphotype-based approaches, or spatially sparse physical samples. This complicates the synthesis of compositional information and may introduce biases or inconsistencies in datasets.

Recommendations for advancing understanding of composition in the deep sea

- *Adopt nested, multiscale survey frameworks:* implement stratified and hierarchical designs across abiotic heterogeneity to capture and quantify both fine-scale patchiness and broad gradients.
- *Integrate multidisciplinary datasets*: Combine geological, oceanographic and biological data to generate robust habitat maps that link abiotic heterogeneity with biodiversity. Mapping of benthic communities is essential, but it is ideally integrated with ocean currents and geomorphology.
- *Quantitatively assess heterogeneity:* Use spatial metrics (patch size, patch richness, patch diversity) to quantify compositional patterns across scales.
- *Promote integrative taxonomy:* Combine approaches to estimate biodiversity, such as imagery, physical samples, trait data and genetic data, to capture multiple dimensions of composition.
- *Test appropriate analytical scales:* Assess the precision (i.e., inverse of the variance) and accuracy (inverse of mean error) of ecological parameter estimations, for instance, as a factor of the sample unit size analysed to capture a pattern (see Simon-Lledó et al. 2019a, b; Ardron et al. 2019). This enables more direct comparisons among multiple source datasets, which can be used to optimise future survey designs and sampling effort.

Configuration: how are seascape elements arranged? Recommendations for understanding spatial structure and ecosystem functioning

Background

Configuration describes the spatial arrangement of seascape elements (i.e., their size, shapes and proximity, and the presence of corridors and barriers) (Fig. 2). Configuration can either facilitate or impede the movement of individuals, genes and matter, mediating dispersal, species interactions, and resilience by affecting how species colonise landscapes or disturbances spread (Turner and Gardner 2015; Chambers et al. 2019). Configuration bridges composition (what is present) and connectivity (how those elements interact).

The concept of configuration is rooted in the patch-matrix and patch-mosaic models (Lausch et al. 2015) (Fig. 2). The patch-mosaic model introduced the role of small-scale habitat heterogeneity in sustaining diversity in deep-sea benthic environments (Grassle and Sanders 1973; Grassle 1977). It helps understand biodiversity maintenance in deep-sea systems, linking spatial heterogeneity with ecological processes such as colonisation, competition, niche dynamics, and successional turnover (McClain et al. 2024). Landscape metrics such as patch size, shape, contagion, clumping, edge density, and fractal dimension (Table 2) (Cushman et al. 2008) quantitatively assess heterogeneity from patch-based representations (e.g., habitat maps, imagery). These metrics can facilitate comparisons of deep-sea habitat mosaics and monitoring of structural change.

Configuration in the deep sea

At megahabitat scales, larger topographic features (Table 2) act as isolated "patches" embedded in a broader abyssal matrix (Fig. 1), following island biogeography principles (MacArthur and Wilson 1967). Their size, character and layout influence population structure, dispersal pathways and turnover (McClain and Hardy 2010; Weston et al. 2022) and the genomic landscape of species. For instance, some hydrothermal vent fields host endemic species restricted to single localities (Thomas et al. 2021; Diaz-Recio Lorenzo et al. 2023). Conversely, vents organised along ridges and in close proximity may operate as stepping stones and facilitate gene propagation across enormous distances (Teixeira et al. 2012; van der Heijden et al. 2012; Breusing et al. 2016).

Within features, the spatial arrangement of patches also matters. Mosaics of topographic complexity, seafloor characteristics, nutrient supply and bottom water parameters within subduction trenches generate substantial heterogeneity (Stewart and Jamieson 2018; Kolbusz et al. 2024), which can leave signatures detectable in population structure*: Alicella gigantea* amphipod populations show local adaptation to varying resource regimes (Chen et al. 2024), while populations of *Hirondellea gigas* amphipod maintain gene flow across neighbouring trenches, yet show signs of local adaptation (Zhang et al. 2025). Configuration effects are also expressed at macro- to micro-habitat scales. Polymetallic nodule fields vary from evenly spaced, large facies to highly clumped, small nodule aggregations, with nodule size and spacing influencing local megafaunal density and diversity (Fleming et al. 2025). Abrupt habitat boundaries can create "edge effects", such as dense aggregations of spherical biogenic tests around isolated boulders in sedimentary environments (Bond et al. 2023).

Biological responses to seascape structure

Responses to composition and configuration are strongly taxon-, habitat- and scale-dependent. Seascape structure interacts with environmental and biotic filtering and life-history traits such as mobility, larval duration, body size and substrate preferences, and stochastic processes, altogether determining where species can persist and how communities are structured (Vellend 2010; Chase and Myers 2011; Quattrini et al. 2017). These patterns differ depending on whether they are examined at basin, kilometre or metre scales, and processes may not be relevant at all scales (Wiens 1989; Levin 1992; Ullmann et al. 2025).

A geomorphic feature can act as either a corridor or a barrier depending on animal traits. Ridges facilitate the propagation of hydrothermal shrimps, mussels and gastropods, but work as barriers for other organisms, such as worms (Plouviez et al. 2010) and isopods (Riehl et al. 2018). Similarly, the availability of hard substrata in abyssal mud beds can control sessile invertebrates that rely on this resource for dispersal and propagation (Simon-Lledó et al. 2025). Engineering species can modulate biotic interactions and act as niche filters. For example, the distribution and abundance of ecosystem engineers such as sponges, corals, and xenophyophores can determine the availability of habitat for associated fauna (Buhl-Mortensen et al. 2010). Similarly, predator–prey interactions influence boundaries in a realised niche. Fine-scale spatial faunal patterns may also reflect historical processes and population dynamics (Susini et al. 2025). However, except for ongoing progress in vent populations (Alfaro-Lucas et al. 2020), our knowledge of life-history traits, biotic filtering, and species interactions at abyssal and hadal depths remains extremely limited.

Key gaps

1. *Limited quantitative use of metrics:* although heterogeneity is well recognised, few studies apply quantitative landscape metrics (e.g., patch size, shape indices, contagion, fractal dimension) to resolve the ecological effects of spatial heterogeneity (Teixidó et al. 2002; Robert et al. 2014; Ismail et al. 2018; Swanborn et al. 2022a). As a result, relationships between habitat geometry, species occurrence and ecosystem functioning remain largely untested.
2. *Trait data scarcity* (Raunkiæran shortfall): Information on the functional traits of deep-sea organisms remains sparse (e.g., feeding mode, body size, mobility, foraging or reproductive strategy), limiting our understanding of how an animal responds to seascape structure and ecosystem functions (Beauchard et al. 2023).
3. *Biotic interactions data scarcity* (Eltonian shortfall)*:* Limited data and knowledge about interactions (e.g., competition, predation, commensalism and symbiosis) among species or groups of species exist, hindering assessments of how interactions shape spatial distributions and responses to spatial structure.

4. *Limited integration of structure and function:* Limited integration and combination of the above (environmental filtering, trait-based responses and biotic filtering) to robustly connect spatial configuration with ecological processes is currently hampered by the lack of multiparametric data sources.

Recommendations

To enhance understanding of configuration, we recommend:

– *Apply spatial metrics systematically*: Broaden the application of seascape metrics (e.g., patch size, shape, contagion, aggregation) to characterise deep-sea mosaics quantitatively. These enable comparisons of habitat geometry, heterogeneity and fragmentation across features or regions (when mapping is carried out consistently), provide baselines for monitoring changes in spatial structure through time and form the basis for resolving the ecological consequences of spatial heterogeneity.
– *Adopt multi-scale and spatially explicit analytical approaches:* Test how spatial patterns and biological responses vary across scales to discern scale-dependent drivers. Simulation frameworks and network-based approaches (e.g., metacommunity or distance–decay models) can test how different patch arrangements influence turnover, connectivity and resilience under climate change and anthropogenic impact.
– *Integrate trait-based data*: By overlaying functional information on habitat maps, we can begin to see the functional heterogeneity of a seascape, which can improve predictions of ecosystem functioning as traits are directly linked to ecological processes. Linking configuration to organismal traits will clarify how spatial structure filters biodiversity and determines which taxa persist under different patch arrangements.
– *Incorporate biotic interactions*: Integrate biotic interactions into spatial analyses to understand community structure and patterns of betadiversity (amount of differentiation between community composition) across seascape configurations. For instance, incorporating analyses of deep ocean food-webs and carbon cycling (e.g., Simon-Lledó et al. 2023b; Stratmann et al. 2023, 2025; Hoving et al. 2023) along with modern computing method*s to* detect non-random species co-occurrence trends (e.g., Pollock et al. 2014).
– *Explore the use of ecological indices to link structure and function:* Explore index-based approaches (e.g., based on Ecological Quality Ratio (EQR), scoring from 0 to 100 for easy comparison) to combine biological attributes with structural and impact indicators across scales (as developed from imagery for mesophotic systems, Cánovas-Molina et al. 2016; Enrichetti et al. 2019).

Connectivity: how are systems linked? Recommendations for understanding gene flow, dispersal, life history and population structure

Background

Ecological connectivity encompasses the flow of energy, matter, genes, propagules, or individuals among populations, communities, or ecosystems (Beger et al. 2022) (Fig. 2). These linkages underpin persistence, resilience, and recovery from disturbance, as well as genetic diversity and speciation (Cowen and Sponaugle 2009; Hilário et al. 2015). Two broad dimensions are typically recognised: structural connectivity, which is related to patch elements (composition) and how they are arranged (configuration), and assesses potential rather than realised connections; and functional connectivity, which represents realised movements and their demographic or ecological outcomes, such as population persistence (Metaxas et al. 2024).

In landscape ecology, structural connectivity is often defined as the degree to which the environment facilitates or impedes movement—termed resistance (Zeller et al. 2012). This concept translates to the deep sea, where resistance arises from habitat composition and configuration (Calabrese and Fagan 2004; Pittman 2017), shaped by geological history, seabed topography, and the physical structure of the water column and currents across micro- to mega- spatial scales (Fig. 2). Although generally lower than on land, resistance increases where geomorphic features such as fracture zones, subduction trenches, seamounts, and axial valleys of mid-ocean ridges interrupt the seafloor continuity and redirect bottom currents, generating vertical gradients in pressure, temperature, and flow. Resistance may also result from sharp physicochemical (e.g., CCD, oxygen minimum zones) transitions in the structure of the water column. These discontinuities may impede the movement of materials (such as nutrients), energy (such as food particles) or individuals (such as larvae or adults), while features such as eddies, boundary currents, and upwelling can also impede or conversely enhance exchange (Metaxas et al. 2024). Abrupt breaks in depth and horizontal isolation shape genetic structure even across broad distances (Taylor and Roterman 2017). In more uniform environments, such as abyssal plains, where distinct boundaries are minimal, distance and habitat availability become key determinants of structural connectivity.

Functional connectivity depends on movement mode, duration, timing and vertical behaviour. Broader syntheses suggest that dispersal in deep-sea species varies with life history and habitat (Hilário et al. 2015; Baco et al. 2016). However, despite taxon-specific variation, two common patterns among deep-sea species are a greater potential for long-distance dispersal (Baco et al. 2016; Simon-Lledó et al. 2025) and the presence of depth-related barriers that structure population connectivity (Jennings et al. 2013; Taylor and Roterman 2017; Galaska et al. 2021). For sedentary taxa, connectivity is largely governed by passive transport during early-life stages, with vertical position in the water column, larval duration, and timing of release strongly influencing dispersal trajectories (Hilário et al. 2015; Gary et al. 2020; Guy et al. 2025). At present, most studies have estimated potential structural connectivity for these species using biophysical models that simulate larval dispersal based on ocean circulation and developmental traits. For motile species, movement distance and direction have been measured using telemetry; however, this is constrained by limited viable technologies (Armstrong et al. 1992; Bagley and Priede 1997) or on short-range spatial observation using imagery (Stratmann et al. 2018; Hovikoski et al. 2025).

Genetic evidence shows that historical factors such as past climate oscillations, geological events, and long-term population isolation interact with contemporary ecological processes like dispersal, recruitment, and selection to determine present-day genetic structure. For instance, in species with large effective populations, *panmictic inertia* can maintain genetic similarity long after reproductive isolation, because as population size increases, genetic drift weakens (Kliman et al. 2008; Piertney et al. 2023). Conversely, broadcast spawners often exhibit *chaotic genetic patchiness*, where local differentiation exceeds large-scale variation due to sweepstake reproduction, collective dispersal, and temporal fluctuations in recruitment (Eldon et al. 2016).

Key gaps

Resolving patterns of realised connectivity in the deep sea remains challenging due to vast spatial scales (Fig. 1), poorly characterised environmental heterogeneity, and limited empirical data (Baco et al. 2016; O'Hara et al. 2025).

1. *Sampling gaps and taxonomic bias*: limited spatiotemporal coverage exists on relevant aspects such as source populations, timing of spawning and larval duration (Hilário et al. 2015; Baco et al. 2016). Most connectivity data are for a few sedentary taxa, such as corals or barnacles, while mobile and soft-bodied fauna remain largely unstudied. This imbalance limits understanding of how active dispersal, trophic interactions, and life-history complexity shape connectivity, and molecular studies therefore often capture historical rather than contemporary patterns. Small sample sizes and uneven spatial coverage further reduce statistical power to detect fine-scale genetic or demographic structure (Lacey et al. 2018; O'Hara et al. 2025).
2. *Limitations of larval transport models*: Both physical and biological components remain constrained. Ocean circulation models often lack validation or sufficient resolution beyond 3000 m depth, while trait data (see Gap 1 above) for early life stages are sparse, forcing reliance on scenario-based assumptions (Metaxas and Saunders 2009; Hilário et al. 2015; Gary et al. 2020; Portanier et al. 2023; Guy et al. 2025).
3. *Technological issues with telemetry:* Telemetry and time-series observations provide valuable insights into functional connectivity through quantification of large-scale movements and

cross-habitat linkages in mobile fauna, but remain restricted by pressure tolerance, short transmission range, and limited deployment duration (Armstrong et al. 1992; Bagley and Priede 1997; Stratmann et al. 2018; Hovikoski et al. 2025).

4. *Genomic gaps:* Inferences often rely on mitochondrial or limited nuclear loci, which may not capture contemporary processes (Vrijenhoek 2010; Taylor and Roterman 2017). Emerging molecular tools such as eDNA offer new opportunities to detect species in poorly sampled regions and to assess population diversity and demographic structure (Adams et al. 2019; Sigsgaard et al. 2020; Takahashi et al. 2023; Nester et al. 2024) but remain constrained by sampling challenges and sparse genomic reference databases (Duhamet et al. 2023).
5. *Temporal gaps:* Most studies represent single surveys, yet larval flux and recruitment can vary markedly over weeks to months, and preliminary data suggests reproduction likely takes place at different seasons for different taxa (Kersten et al. 2017). Without sustained time-series data, it remains difficult to distinguish episodic dispersal from ongoing gene flow or to assess how disturbance and environmental change alter connectivity dynamics.

Recommendations

A mechanistic view of connectivity requires linking structural assessments (composition, configuration) with functional information (movement, recruitment and genetics), integrating genomics and biophysical modelling.

- *Holistic structural maps:* integrate benthic habitat maps representing composition and configuration to estimate structural connectivity with ocean currents and geomorphology, which act as both pathways and barriers to dispersal and are critical for identifying potential sources and sinks, and for producing realistic estimates of potential connectivity.
- *Validation of hydrodynamic models:* validate existing hydrodynamic models at abyssal and hadal depths, e.g., comparing in-situ data from moorings with global models. Improve the resolution of circulation models by integrating global models with in-situ data from moorings, gliders, ADCPs, and deep floats. Modernise existing ocean circulation models to routinely include depths beyond 6000 m and to provide sufficient vertical resolution in the benthic boundary layer.
- *Build standardised trait and metadata catalogues:* compile and standardise existing data on larval and early-life traits (e.g., duration, vertical distribution, behaviour, and development) to better parameterise dispersal models and reduce assumptions. Scenario-based approaches can address remaining gaps, while aggregating laboratory, field, and molecular records provides a critical foundation. Emerging molecular tools (eRNA, hybrid capture sequencing of eDNA), which can detect gene-expression patterns or developmental markers, may help resolve larval condition or stage in situ (Pochon et al. 2017; Yates et al. 2021; Li et al. 2023).
- *Life history reconstruction techniques*: Apply otolith microchemistry and growth-ring analysis to trace individual movement histories (Gerringer et al. 2018), and combine stable-isotope data with genomic assignments (e.g., SNPs, coalescent modelling) to resolve population structure, demographic change, and realised connectivity.
- *Empirically validate supply and settlement:* Deploy artificial settlement structures (e.g., ARMS units or moored collectors) to measure colonisation and settlement rates visually or via collected samples (e.g., Meyer-Kaiser et al. 2019; Strong et al. 2023).
- *Advance telemetric technologies at depth:* Improved data transmission and in-situ tagging now enable animal tracking in extreme environments (Edwards et al. 2019). Autonomous vehicles and long-endurance landers (e.g., Orpheus AUV, SubC lander) support tag deployment and extended monitoring, while submersible-based methods have successfully tagged large demersal species such as coelacanths (Schauer et al. 1997) and sixgill sharks (OceanX 2019). Ingestible acoustic tags (e.g., CAT tags) are effective at abyssal depths (Bagley and Priede 1997). Ongoing advances in acoustic positioning and communication (e.g., JAMSTEC platforms) will further

enhance long-term tracking and behavioural studies.

Context: what forces shape these systems? Environmental and biotic drivers and constraints

Background

Context refers to the broader settings—environmental and biological—that influence and are connected to local habitat patches (Fig. 2). Context spans global to local scales and is the matrix in which patches exist and the background against which composition, configuration, and connectivity should be considered. Environmental context includes surrounding environments, including those at the same depth (e.g., near bottom currents (Aller 1989), water properties (Rakka et al. 2025), geological disturbances (Ueda et al. 2023), vertical exchanges and episodic inputs such as fluxes from surface waters (e.g., surface productivity Smith et al. 2006; Johnson et al. 2007)) and even input from terrestrial systems (e.g., river flows (Talling et al. 2022), and pollutants (Takada et al. 1994; Jamieson et al. 2017)). Biotic context refers to phylogenetic and biotic filters that determine how organisms occupy their environment, such as biological interactions (e.g., Stevenson et al. 2015).

Excluding contextual information risks attributing biodiversity patterns solely to depth or local factors. Even when contextual variables cannot be measured directly, recognising context enables sharpened ecological inferences. For example, species–area relationships are strengthened when habitat size is considered alongside food availability (Haedrich 1985). It also allows dialogue about the relative influence of key drivers, for example, the interplay between temperature, depth, and POC flux (Bond et al. 2023; Swanborn et al. 2025).

Environmental context

Ocean properties exert strong control on composition, with deep-water masses (oxygen, temperature, carbonate chemistry) and associated geochemical boundaries such as the carbonate compensation depth (CCD) shaping biogeographic transitions (Simon-Lledó et al. 2023a, b), and varying between and within hadal features (Kolbusz et al. 2024). Energy availability, largely represented by POC flux and temperature, is a pervasive contextual driver (McClain et al. 2012) and minor declines in POC can yield significant reductions in benthic faunal abundance or biomass (Ruhl et al. 2008; Billett et al. 2010; Durden et al. 2015), while small temperature changes ($\leq$0.1–0.5° per decade) can cause shifts in community structure (Yasuhara and Danovaro 2016). Palaeoecological records indicate that over longer timescales, temperature may become the dominant control on diversity (Yasuhara and Danovaro 2016).

Biodiversity patterns reflect broad-scale environmental filtering and spatial gradients related to energy limitation (McClain et al. 2012; Alfaro-Lucas et al. 2020; Simon-Lledó et al. 2025). Diversity typically declines with depth and towards the poles, attributed to decreasing POC or temperature (Woolley et al. 2016; Carter et al. 2025), though patterns vary among ocean basins and taxonomic groups (McClain et al. 2012, 2024). Deep-sea species often exhibit wide horizontal but narrow vertical (anisotropic) ranges, constrained by steep bathymetric gradients in hydrostatic pressure, carbon flux, and temperature (McClain and Hardy 2010). Relatively horizontally homogeneous abyssal habitats differ from vertically heterogeneous continental slopes or subduction trenches, where variation in carbon flux, topography, sediment type, and current regimes creates complex, patchy distributions (Carney 2005; Zardus et al. 2006; Levin and Dayton 2009; Stewart and Jamieson 2018). Horizontal ranges tend to broaden with increasing depth, consistent with early observations that species occupy larger geographic extents where environmental conditions are more stable and uniform (Wilson and Kaufmann 1987; Allen and Sanders 1996). Yet, distance-decay patterns highlight measurable beta-diversity turnover at broad scales linked to dispersal limitations (McClain et al. 2012; Simon-Lledó et al. 2025), revealing seemingly homogeneous abyssal plains still harbour contextual structuring processes, often detectable at multiple scales (Simon-Lledó et al. 2020), although not necessarily evident across all taxonomic or functional groups (Drazen et al. 2021).

Biotic context

Biotic context defines the evolutionary and ecological capacities that determine how species occupy, persist in and modify environmental space. Phylogenetic relationships reflect long-term outcomes of processes such as environmental filtering or other forces driving adaptation (e.g., competitive exclusion) (O'Hara et al. 2019). Trait conservation explains persistent under particular environmental conditions, observed for instance in studies of octocoral communities in the Gulf of Mexico, while stochastic colonisation and dispersal limitation can generate random assemblages within comparable patches (Quattrini et al. 2017). Biotic interactions—predation, competition and facilitation—further modulate community assembly, yet remain poorly resolved for most deep-sea taxa (Allcock and Johnson 2019).

Disturbance, stochastic processes and patch dynamics

Disturbance (e.g., earthquakes, landslides, mass flows, pulse inputs) is a key contextual component, capable of altering habitats and resetting successional trajectories (Harris 2014; Mountjoy et al. 2018; Swanborn et al. 2025). Recovery is highly variable, ranging from recolonisation (Bigham et al. 2023) to little recovery decades after disturbance (Simon-Lledó et al. 2019b; Jamieson et al. 2022; Jones et al. 2025). Recent synthesis work in abyssal polymetallic nodule environments demonstrates that habitat heterogeneity and disturbance regimes jointly influence benthic community structure across size classes (Ullmann et al. 2025). Specialisation of abyssal and hadal fauna to extreme, oligotrophic and stable conditions (Brown and Thatje 2014) may increase vulnerability to disturbance, such as resulting from climate change (Sweetman et al. 2017; Harris et al. 2023) or seabed mining (Simon-Lledó et al. 2019b), raising questions regarding resilience and the development of alternative stable states. Stochastic mechanisms also drive abrupt shifts (Chase and Myers 2011), and while some of such mechanisms have been identified in the deep ocean (landslides, food-falls, nutrient pulses, or benthic storms), the scarcity of temporal series has almost certainly limited our current understanding of the many other potential factors that can yield sudden ecological drifts on abyssal and hadal ecosystems.

Patch dynamics (Wu and Loucks 1995) link disturbance, stochasticity and recovery. Seascapes operate as shifting mosaics of patches at different successional stages, driven by disturbance frequency, intensity and recovery, interacting with background drivers such as POC and temperature, and rarely being in equilibrium (Frederick Grassle and Sanders 1973). Persistence reflects a balance between colonisation and extinction, with connectivity mediating recolonisation potential (Hanski 1994). The evolutionary trajectory of a disturbed community towards a pre-disturbance or alternate stable state depends on context, traits, and connectivity, determining which taxa persist under given structural conditions.

Key gaps

A major challenge in deep-sea ecology is disentangling the relative influence of historical and environmental filtering (context), dispersal limitation, and trait-mediated responses to environmental structure. Despite its importance, the role of context in deep-sea systems is still poorly resolved, primarily due to several key research gaps.

1. *Lack of temporal resolution*: Sparse time series data for deep-sea ecosystems limit our ability to separate natural fluctuations (e.g., seasonal or interannual variability, responses to episodic events or natural disturbance) from anthropogenic change (Koslow and Couture 2015; Meyer-Kaiser et al. 2025) or inform modelling efforts (Karl 2010). While some impressive long-term observatories exist (e.g., PAP-SO, ONC, SOTS, PMEL stations), and programs like Argo floats have shown what can be achieved with long-term monitoring of physical variables, a similar effort is needed for biological and ecological data.
2. *Limited integration across datasets*: ecological surveys are often disconnected from contextual information such as food flux, carbonate chemistry or disturbance histories, nor do they bridge the mismatch between local-scale observations and wider-scale processes, perpetuating scale mismatch and constraining comparability.
3. *Disturbance and recovery pathways:* few studies systematically capture pressures, disturbances and recovery in the deep sea (Ullmann et al. 2025). Disturbance quantification is often opportunistic (see Bigham, 2023) or requires a Before-After-Control-Impact design which is difficult to execute in the deep ocean. These knowledge gaps not only limit our ability to understand resilience, recovery and natural variation in the deep sea, but

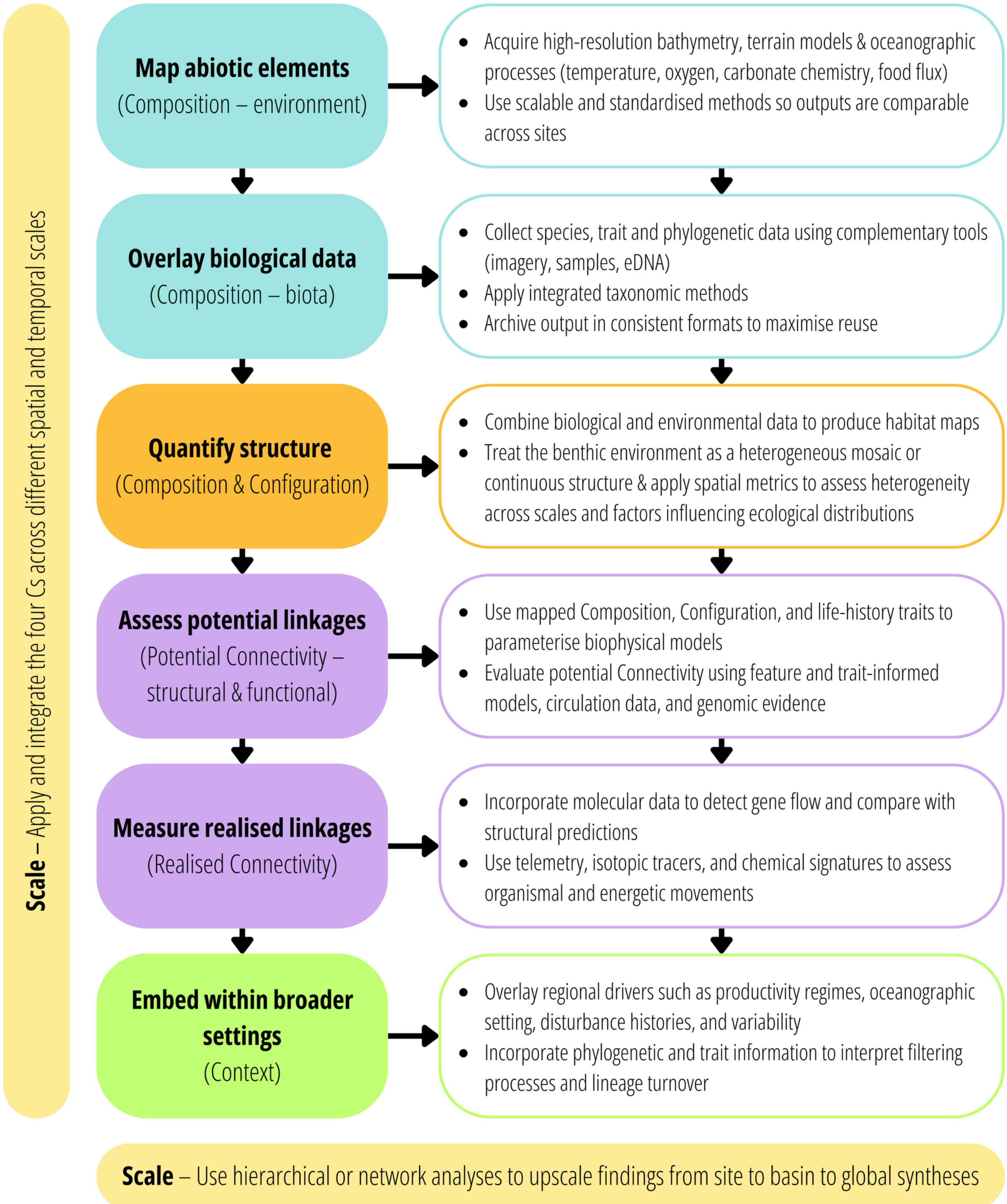

Fig. 3 Proposed workflow for deep seascape ecology. Colours are representative of each concept (Composition, Configuration, Connectivity and Context)

also limit accurate forecasting of climate-related change.

4. *Knowledge about the influence of phylogenetic relationships:* limited phylogenetic information on many species exists (Darwinian shortfall; see Hortal et al. 2015) in a community and models that utilise these data specific to deep-sea environments.
5. *Lack of global synthesis:* No comprehensive meta-analysis of deep-sea biodiversity patterns exists, equivalent in scope to the syntheses of abundance and biomass provided by Rex et al. (2006) and Wei et al. (2010). Such a synthesis is critical for resolving global drivers of diversity and establishing baselines for future change.

Recommendations

- *Expand long-term time series:* Integrating time-series data from moorings, autonomous sensors, and global ocean models can provide some of the necessary temporal context to distinguish natural fluctuations from long-term trends.
- *Integrate multi-scale and multi-disciplinary datasets:* compile multi-scale and multi-dimensional environmental datasets that include key abiotic factors such as food flux, oxygen levels, temperature, carbonate chemistry, geochemical and sedimentation, and explicitly couple these with faunal surveys, biological data (isotope analysis, phylogeny, traits etc.).
- *Track disturbance and recovery:* explicit inclusion of episodic disturbance events (e.g., turbidity flows, seismic activity) and the biological response to these disturbances is an important step in modernising theories of resilience, recovery, speciation and turnover in the deep sea.
- *Embed biotic context:* develop deep-sea phylogeny and trait-catalogues for major groups
- *Establish integrated baselines and conduct meta-analyses*: Leverage the dispersed but extensive archive of deep-sea sampling conducted over nearly eight decades across basins, depths, and spatial scales to synthesise the global drivers of deep-sea diversity, accounting for methodological and taxonomic differences using appropriate statistical frameworks. Combined with field data, build integrated baselines across deep-sea habitats – including trenches, fracture zones and abyssal plains – to understand ecosystem and fauna resilience to pressures and build robust scenario models to forecast future changes under various climate and anthropogenic pressures.

Future directions and strategic needs

The Cs provide a conceptual foundation for understanding biodiversity-environment relationships, including in the deepest parts of the world's oceans (Fig. 1). While each captures a distinct concept, they are tightly interrelated (Fig. 2). Composition defines what is present, Configuration arranges these elements in space, Connectivity determines how they interact, and all three are embedded in Context: the broader environmental, biotic, and temporal setting that modulates expression (Fig. 2).

Specific challenges are evident for each C, but common themes emerge across all, indicating strategic priorities for advancing seascape ecology in abyssal and hadal environments from concept to practice. Challenges in linking structural patterns with functional outcomes will require coordinated advances across biological, physical, and technological domains.

Common strategic themes

1. *Scale as a unifying principle*: Across all sections, scale emerges as both a challenge and an opportunity.
2. Adapt multi-scale designs that capture fine-scale patchiness while also situating results in a basin or global scale context
3. Explicitly adopt scale in analysis to enable cross-site comparisons and model scale-dependent relationships
4. *Integration and interdisciplinarity:* Each C stresses a need for synthesis. Composition requires integrated bathymetric, oceanographic, and biological data to delineate seascape units; configuration assesses the spatial mosaics resulting from this process; connectivity overlays traits and genomic information; and context couples this with broader environmental and biotic processes and long-term data.

5. Design surveys to maximise multi-purpose returns
6. Develop interoperable, multidisciplinary datasets and shared standards that allow data sharing and joint, collaborative analyses across locations
7. Foster collaboration across biology, ecology, geology, oceanography, data science, and technology.
8. *Trait-based, phylogenetic and functional approaches*: Traits determine how species interact with the environment, tolerate contextual gradients, and contribute to ecosystem function, while evolutionary history constrains present-day patterns. Yet, trait and phylogenetic data remain sparse for most abyssal and hadal taxa.
9. Build trait catalogues with life-history traits to develop functional databases for deep-sea organisms
10. Generate reference libraries with phylogenetic information to assess evolutionary constraints
11. *Temporal and disturbance dimension:* Temporal dynamics and disturbance legacies remain among the least resolved elements of deep-seascape ecology. Without time-series, it is impossible to distinguish natural variability from directional change or response to an ephemeral disturbance.
12. Expand long-term observational networks and autonomous monitoring to capture interannual and decadal variability.
13. Explore the relationship between records of chronic or ephemeral disturbance and recovery trajectories to understand resistance, resilience and potential alternative stable states.
14. *Technological innovation*: Progress hinges on technological advances that extend depth, duration, and resolution of observation
15. Invest in pressure-tolerant sensors, autonomous imaging, and sampling platforms; next-generation molecular and isotopic tools; and deep-capable telemetry and acoustic networks.
16. *Standardisation and interoperability:* Spatial inconsistencies in research extent and effort pose a barrier to the advancement and integration of data for a holistic understanding of deep seascapes.
17. Promote innovation in sampling design that is scalable, standardised, and spatially extensive
18. Adopt open, FAIR (Findable, Accessible, Interoperable, Reusable) data principles where possible to accelerate cumulative knowledge building.
19. Promote data sharing and collaboration
20. *Extending seascape ecology to the pelagic realm:* Investigation of how the Cs could be applied to the water column, particularly the dynamic 3D nature of this environment and its inhabitants.
21. Develop frameworks and metrics for pelagic composition, configuration, connectivity, and context, linking physical structure (e.g., water-mass fronts) with biotic patterns.

To translate the Cs from concept to implementation, we propose an iterative workflow (illustrated in Fig. 3) that builds from mapping the physical template to integrating biological, functional, and temporal dimensions. Together, these steps integrate the Cs to advance deep-seascape ecology from conceptual foundation to operational practice.

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Declarations

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