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Shaping research in marine functional connectivity for integrated and effective marine science and management

Audrey M. Darnaude[1,*], Susanne E. Tanner[2], Andreu Blanco[3], Anna M. Sturrock[4], Yael Teff Seker[5], Angel Pérez-Ruzafa[6], Jonne Kotta[7], Tamar Guy-Haim[8], Francisco R. Barboza[7], Manuel Hidalgo[9], Katell Guizien[10], Jerneja Penca[11], Lucía López-López[12], Maria Beger[13,14], Federica Costantini[15], Sophie Arnaud-Haond[16], Cynthia Riginos[17], Kris Hostens[18], Gil Rilov[8], Stelios Katsanevakis[19] and Ewan Hunter[20]

[1]*MARBEC, Univ. Montpellier, CNRS, IRD, Ifremer, Montpellier, France*
[2]*MARE – Marine and Environmental Sciences Centre, Department of Animal Biology, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Lisboa 1749-016, Portugal*
[3]*Centro de Investigación Mariña, Future Oceans Lab, Torre Cacti, Universidade de Vigo, Campus Lagoas Marcosende, Vigo 36310, Spain*
[4]*School of Life Sciences, University of Essex, Wivenhoe Park, Colchester, CO4 3SQ, UK*
[5]*Department of Sociology, 1283 Social Sciences and Humanities, University of California, Davis, California, CA 95616, USA*
[6]*Department of Ecology and Hydrology and Campus of International Excellence 'Mare Nostrum', University of Murcia, Murcia 30100, Spain*
[7]*Estonian Marine Institute, University of Tartu, Mäealuse 14, Tallinn 12618, Estonia*
[8]*National Institute of Oceanography, Israel Oceanographic and Limnological Research, PO Box 8030, Haifa 31080, Israel*
[9]*Spanish Institute of Oceanography (IEO, CSIC), Balearic Oceanographic Center (COB), Ecosystem Oceanography Group (GRECO), Moll de Ponent s/n, Palma 07015, Spain*
[10]*CNRS, Sorbonne Université, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB, Observatoire Océanologique de Banyuls, Avenue Pierre Fabre, Banyuls-sur-Mer F-66650, France*
[11]*Science and Research Centre Koper, Mediterranean Institute for Environmental studies, Koper, Slovenia*
[12]*Oceanographic Centre of Santander, Spanish Institute of Oceanography, Severiano Ballesteros 16, Santander 39004, Spain*
[13]*School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK*
[14]*Centre for Biodiversity and Conservation Science, School of Biological Sciences, University of Queensland, Brisbane, QLD 4072, Australia*
[15]*Laboratorio di Ecologia sperimentale, Department of Biological, Geological and Environmental Science, UOS Ravenna, Università di Bologna, via S. Alberto, 163, Ravenna 48123, Italy*
[16]*MARBEC, Univ. Montpellier, Ifremer, CNRS, IRD, Sète, France*
[17]*School of the Environment, The University of Queensland, 280-284 Sir Fred Schonell Dr, St., Lucia, QLD 4072, Australia*
[18]*Flanders Research Institute for Agriculture, Fisheries and Food (ILVO-Marine), InnovOcean Campus, Jacobsenstraat 1, Oostende 8400, Belgium*
[19]*Department of Marine Sciences, University of the Aegean, University Hill, 2.16, Mytilene 81100, Greece*
[20]*Agri-Food & BioSciences Institute, Newforge Lane, Belfast, BT9 5PX, UK*

ABSTRACT

Effective knowledge of ecological connectivity at sea and at the land–sea interface is key to supporting global policy goals to conserve and restore ocean biodiversity and function. However, a persistent lack of commonality in terminology and understanding around the concept of connectivity in marine ecological studies hampers its integration across disciplines, and its application in spatial planning and policy. Building on an extensive literature review, we clarify definitions and

* Author for correspondence (Tel.: +33(0) 467 144 744; E-mail: audrey.darnaude@cnrs.fr).

subcategories of marine connectivity, and propose a unified conceptual framework for Marine Functional Connectivity (MFC) research to support the integration of multidisciplinary scientific knowledge into management and policy. We identify key challenges and future directions for advancing this emerging field, bringing together most strands of marine science to understand changes in biodiversity and functional interdependencies between habitats and regions. Embedding this new integrated MFC research at the core of marine environmental science promises to improve significantly predictions of environmental and socio-economic change and the sustainable use of ecosystems and resources at sea and at the land–sea interface.

Key words: marine biodiversity, marine resources, functional ecology, marine spatial planning, ecosystem services, environmental conservation.

CONTENTS

I. INTRODUCTION

Marine ecosystems are under growing and unprecedented threat from diverse anthropogenic pressures acting at local, regional, and global scales (Halpern *et al.*, 2019; Jouffray *et al.*, 2020; IPCC, 2022). Yet, they deliver multiple services that are essential to our societies and the global health and functioning of the biosphere (IPBES, 2019; Selig *et al.*, 2019; FAO, 2020). Sustainable management of marine ecosystem resources is vital to halt ongoing global biodiversity loss (IPBES, 2019), mitigate climate change impacts (IPCC, 2022), and meet UN Sustainable Development Goals for 2030 (OECD, 2022). To shift the global trajectory away from further degradation of marine biodiversity and ecosystem services (Mace *et al.*, 2018; IPBES, 2019; IPCC, 2022), ambitious conservation targets have been set (Hilty *et al.*, 2020; Williams *et al.*, 2021). However, marine conservation and sustainable management efforts to date have often prioritized the most straightforward measures, typically focussing on highly visible single issues or iconic species (e.g. identifying biodiversity hotspots, mapping the distribution of target species, or reducing plastic pollution and bycatch). This focus overlooks the fundamental underlying ecological processes that link ecosystems and ultimately enable resilience to environmental stressors. In the current era of environmental crises, urgent action is required to shift course and address this critical gap (Folke *et al.*, 2021; Halpern *et al.*, 2023).

In ecology, the concept of 'connectivity' refers to the extent to which spatially distinct populations, communities, habitats, or ecosystems are linked by the exchange of genes, organisms, nutrients, materials and energy (Balbar & Metaxas, 2019; Hilty *et al.*, 2020; Cannizzo, Lausche & Wenzel, 2021). Connectivity sustains life on Earth by mediating the complex interactions between species or communities and the functioning of the ecosystems they inhabit (Hillman, Lundquist & Thrush, 2018; Cannizzo *et al.*, 2021). Therefore, preserving connectivity is crucial for conserving the ocean and its resources (Beger *et al.*, 2010; Wood *et al.*, 2022), especially given the sensitivity of marine systems to global change (Magris *et al.*, 2014; Andrello *et al.*, 2015; Lima *et al.*, 2021). The importance of connectivity is beginning to emerge in global governance, as illustrated by the global target to protect 30% of terrestrial and marine realms 'through ecologically representative, well-connected and equitably governed systems of protected areas and other effective area-based conservation measures' (CBD, 2022, p. 9). A growing number of publications also advocate the integration of connectivity data into marine spatial planning (e.g. Carr *et al.*, 2017; Balbar & Metaxas, 2019; Beger *et al.*, 2022) and policy frameworks (e.g. Hilty *et al.*, 2020; Cannizzo *et al.*, 2021; Johansen *et al.*, 2021) at varied scales. However, translating connectivity knowledge to spatial planning is currently hindered by the diversity and complexity of existing connectivity data and management boundaries (Bryan-Brown *et al.*, 2017; Balbar & Metaxas, 2019; Keeley *et al.*, 2022), but also by ambiguous terminology (Lowe & Allendorf, 2010; Olds *et al.*, 2016). Definitions of the many types of 'connectivity' considered in marine ecological studies are not consistently applied, and the methods and terms used to quantify each type of connectivity vary (Grober-Dunsmore *et al.*, 2009; LaPoint *et al.*, 2015; Cramer *et al.*, 2023). As a result, communication issues often arise, as well as debates about the types of connectivity information most needed for ecosystem and resource management (Balbar & Metaxas, 2019).

Historically, ecological connectivity has been divided conceptually into two intertwined components, one 'structural' and one 'functional' (Auffret, Plue & Cousins, 2015). Structural connectivity is considered a general feature of the landscape, linked to its geological and physicochemical characteristics, where heterogeneity and structuring are measured independently of any attributes of living organisms (Collinge & Forman, 1998; Taylor, Fahrig & With, 2006). Functional connectivity, on the other hand, describes the response of living organisms to this environmental variation, encompassing all their movements and exchanges across habitat patches and ecosystems (Tischendorf & Fahrig, 2000). Functional connectivity can be caused, facilitated or hampered by structural connectivity, e.g. through transport by marine currents or physical barriers linked to habitat fragmentation (Lough, Broughton & Kristiansen, 2017). However, the influence of species biology and behaviour often decouples functional connectivity from structural connectivity, resulting in different or even opposite directional linkages, and in rates of exchange that would not occur through passive abiotic fluxes alone (McInturf *et al.*, 2019). Thus, while human activities affect both structural and functional connectivity, it is functional connectivity that ultimately determines the demographic, ecological and evolutionary interdependency of populations and communities, and most of the flow of energy and biomass among ecosystems and habitats (Cowen & Sponaugle, 2009; Lamberti, Chaloner & Hershey, 2010). By either mitigating or amplifying the ecological effects of structural connectivity and environmental change, functional connectivity shapes the fate of species, ecosystems, and their services (Marcos *et al.*, 2021). Understanding functional connectivity is therefore crucial, both for predicting the responses of marine ecosystems to environmental change and for designing effective conservation and management strategies for the ocean.

The adoption of the concept of 'functional connectivity' is a relatively recent development in marine ecology (Darnaude *et al.*, 2022), as illustrated by the limited published work to date (less than 100 papers by the end of 2024) specifically referring to 'Marine Functional Connectivity' (MFC), mostly after 2020 (Fig. 1; see online Supporting Information, Appendix S1, for search strings and methods used). Therefore, our understanding of the general patterns, drivers and consequences of functional connectivity is largely derived from studies in the continental realm (e.g. Keeley *et al.*, 2018; Wood *et al.*, 2022), with little comparable information about marine systems (Saunders *et al.*, 2016; Virtanen, Moilanen & Viitasalo, 2020; Cannizzo *et al.*, 2021). However, a wealth of accumulated knowledge about the distribution and movements of marine organisms exists (>18,700 papers, Fig. 1). Over the past century, an impressive amount of connectivity data has been gathered throughout the world's oceans, using a variety of approaches from various research fields (e.g. genetics, tagging and tracking, natural tags, biophysical modelling). These methods have supported significant advances in MFC knowledge, with connectivity estimates now available for a broad range of aquatic organisms and across all marine ecoregions (Bryan-Brown *et al.*, 2017). However, the various methods and disciplines differ in their underlying hypotheses and assumptions, in the geographical or temporal scales at which they address connectivity (Bryan-Brown *et al.*, 2017), and in the type of connectivity metrics they generate (Balbar & Metaxas, 2019). Obtaining a holistic picture of MFC therefore requires effective aggregation and integration of interdisciplinary data sets, using standardized techniques to meet the information needs of ecological forecasting and decision-making (Darnaude *et al.*, 2022).

The challenge of unifying the field of MFC research goes beyond data integration though, as the word 'connectivity' has historically been used and interpreted differently across disciplines, with the same terms having similar yet divergent definitions (LaPoint *et al.*, 2015). In order to move forward, MFC science requires clarification of its concepts, definitions and contours. There is also a need for an integrated, multidisciplinary framework for the field, effective both in advancing knowledge of the structure and functioning of marine ecosystems and in integrating these data into environmental management and policy. Towards this goal, we first identify the main challenges for advancing global MFC knowledge and using MFC data for decision-making in management and policy. Building on existing definitions and terminology used in marine ecology, we then propose a unified and practical definition of MFC, coupled with an overall conceptual and methodological framework, positioning MFC science at the heart of marine environmental research and management. As illustrated by a few examples, the emergence of this new, multidisciplinary research field is pivotal to push marine research towards greater integration for improved management and conservation of the seas.

II. CHALLENGES FOR CURRENT AND FUTURE RESEARCH ON MARINE FUNCTIONAL CONNECTIVITY

As biodiversity and ecosystem functioning are intrinsically linked (Dahlin *et al.*, 2021), a comprehensive insight into

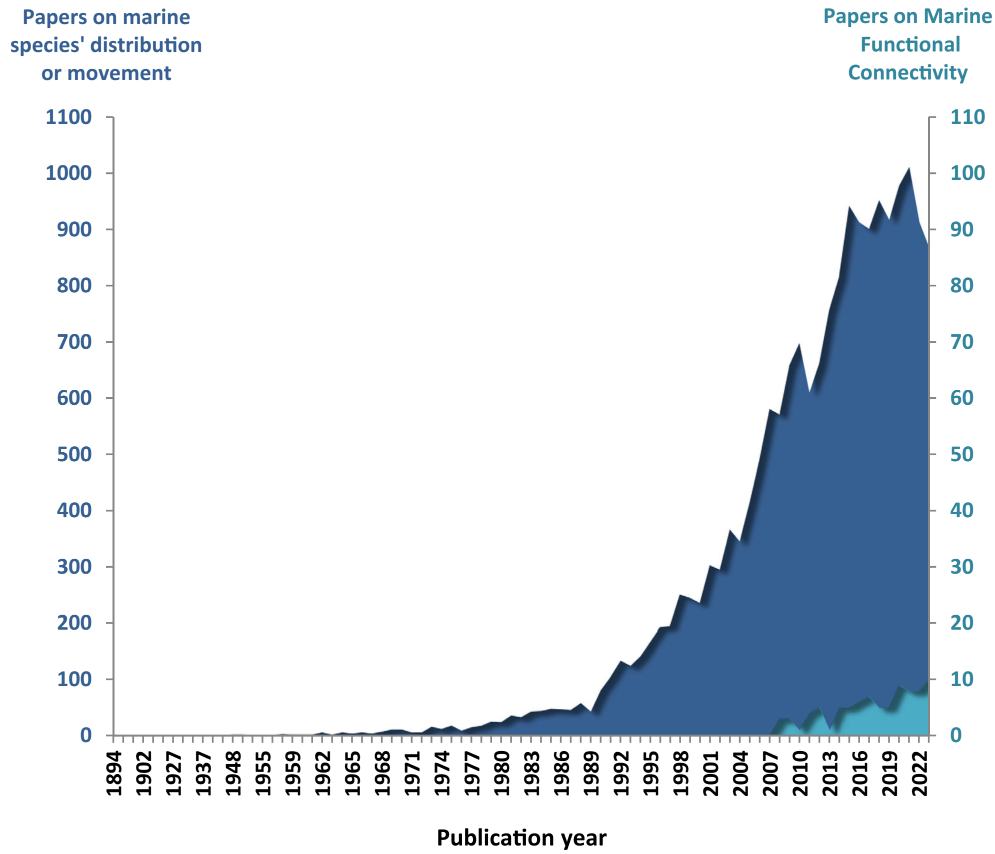

Fig. 1. Number of papers in the Marine Ecology literature published annually since 1894 that either specifically refer to Marine Functional Connectivity (light blue, right axis) or investigate it indirectly (dark blue, left axis). Searches using *ISI Web of Science* and *Scopus* were completed on April 22nd, 2024. For more information regarding the production of this figure, see Appendix S1.

functional connectivity is essential to understand how key ecological functions are maintained across multiple scales and biological realms (Cumming, Magris & Maciejewski, 2022). However, while functional connectivity in continental systems is now sufficiently well described to identify its key drivers and consequences (Martensen, Saura & Fortin, 2017; Hartfelder *et al.*, 2020; Wood *et al.*, 2022), MFC knowledge remains limited and fragmented (Pittman *et al.*, 2021; Cumming *et al.*, 2022). As a result, insights gained from terrestrial ecology still dominate our understanding of how functional connectivity shapes marine ecosystems and the resulting implications for conservation and sustainable resource management (Cannizzo *et al.*, 2021). This poses a significant challenge, as the marked differences between terrestrial and marine systems can result in inappropriate marine management and conservation strategies.

While in theory the same basic principles (e.g. structural and functional connectivity) apply in both realms, the processes that govern connectivity in the ocean are substantially different from those that apply on land (Saunders *et al.*, 2016; Cannizzo *et al.*, 2021). The fluid nature and three-dimensionality of the ocean and its high heterogeneity, shaped by currents, eddies, and other oceanographic and geomorphological processes, make marine species' movement and dispersal far more dynamic and complex (Cannizzo *et al.*, 2021). Life-history strategies and dispersal modes also vary substantially between marine and terrestrial organisms (Robinson *et al.*, 2011; Capdevila *et al.*, 2020). In particular, marine species generally undergo an extensive dispersal phase during their life, most often during their smallest stages, i.e. as eggs and larvae (Burgess *et al.*, 2016; Capdevila *et al.*, 2020). Since, when drifting in the water, even small organisms can be transported over long distances and bypass potential barriers such as habitat discontinuities or bottom topography (Cowen & Sponaugle, 2009), body size is not a predictor of the dispersal potential of organisms at sea (Pineda, Hare & Sponaugle, 2007; Burgess *et al.*, 2016; Villarino *et al.*, 2018). Nonetheless, the general positive relationship between geographic distance and genetic isolation, largely assumed to apply at sea (Palumbi, 2003), is not consistently observed (González-Wangüemert *et al.*, 2004). Behavioural mechanisms often retain larvae near their spawning origin (Selkoe *et al.*, 2016), making self-recruitment in marine populations more common than previously believed (Green *et al.*, 2015). Therefore, inferences about general patterns of functional connectivity at sea are particularly challenging. In addition, the life cycles of many marine organisms involve complex movements, including successive phases of juvenile and adult active migration spanning tens to thousands of kilometres across oceanic provinces, depth zones, and even sometimes realms. These movements can result in significant transboundary transfers of matter, the magnitude of which is only beginning to be appreciated (e.g. Benkwitt *et al.*, 2022; Burd, 2024). Importantly, individual variation in migratory strategies is likely to be more common and complex than previously understood in marine species (Bradbury *et al.*, 2008), but has been poorly studied so far. Beyond impacting on local population dynamics, this intraspecific diversity likely affects species' eco-evolutionary trajectories and community ecology by acting on biodiversity and connectivity at local and global scales (e.g. Durant *et al.*, 2019; Ellingsen *et al.*, 2020).

Identifying the specific mechanisms that drive MFC patterns and their changes will therefore allow a better understanding of how marine species and ecosystems persist due to the flows of individuals, energy, and matter through the seascape. However, barriers to generating and applying this knowledge are multifold. We have categorized them into the three main challenges described in the following subsections.

(1) Integrating research and data across disciplines

Obtaining a global overview of MFC presents several specific difficulties. As vast, open, three-dimensional spaces, marine environments are inherently difficult to access. The small size and high mortality rates of the dispersive stages of most marine species make direct tracking very difficult. Generalizations across taxa are challenging given the wide variation in biological traits such as pelagic larval duration, swimming ability, inter-generation time, and life cycle complexity (e.g. Pineda *et al.*, 2007; Cowen & Sponaugle, 2009; Swearer, Treml & Shima, 2019). Furthermore, some marine species or life stages inhabit or cross several realms, oceanic provinces and/or depth zones, for which observation and sampling tools differ significantly (Benway *et al.*, 2019).

This complexity has led to the development of a vast array of methods to estimate or predict the distribution and movements of marine organisms (Bryan-Brown *et al.*, 2017; Sturrock *et al.*, in press), from microscopic diatoms and bacteria (e.g. Mestre *et al.*, 2018; Šupraha *et al.*, 2022) to large top predators (e.g. Block *et al.*, 2011; Nathan *et al.*, 2022). Most MFC estimates so far have been obtained *via* genetics (e.g. Legrand *et al.*, 2022), natural tags like otolith chemical composition (Reis-Santos *et al.*, 2023), conventional, acoustic or archival tags (e.g. Matley *et al.*, 2022; Welch *et al.*, 2025), and biophysical modelling (e.g. Swearer *et al.*, 2019). Each technique differs in the habitats, life stages and taxa to which it can be applied and has a suite of underlying assumptions, strengths, and weaknesses, which determine the type, spatiotemporal scale, and accuracy of resulting MFC estimates (Bryan-Brown *et al.*, 2017; Keeley *et al.*, 2022). Describing the combined lifetime migrations and cross-generational movements of all marine taxa requires integration of these data and a truly multidisciplinary approach (Darnaude *et al.*, 2022; Tanner *et al.*, 2025).

Data integration among methods has been rare thus far (e.g. Padrón *et al.*, 2018; Pérez-Ruzafa *et al.*, 2019), and largely restricted to combinations between genetics, natural tags and biophysical modelling (Bryan-Brown *et al.*, 2017; ICES, 2023). Attempts to estimate and compare connectivity across multiple species (e.g. Green *et al.*, 2015; Legrand *et al.*, 2022) or to use MFC data to infer higher-level ecological processes, such as biogeochemical fluxes or ecosystem services (Jahnke & Jonsson, 2022), remain scarce. Currently, the main challenge to integrating MFC data across methods is to derive outputs that are both statistically rigorous and biologically meaningful, despite profound differences in units of measurement, spatiotemporal scales, resolutions, error structures, and underlying assumptions (Darnaude *et al.*, 2022; Tanner *et al.*, 2025). Advancing statistical tools for cross-disciplinary data integration (e.g. Gaggiotti, 2017; Chen *et al.*, 2018) will be essential to produce comprehensive estimates of lifetime and transgenerational MFC at the scales of populations, species and communities. The transdisciplinary approach required to tackle MFC comprehensively also poses challenges at the human level, as MFC researchers need to engage with and integrate advances across diverse research fields (Abaunza *et al.* 2008; Tanner *et al.*, 2025). Unifying MFC terminology and definitions (see Section III) and building research capacity across often-siloed research fields is a first step towards achieving truly transdisciplinary MFC science.

(2) Reaching an in-depth understanding of MFC drivers and consequences

While main ocean threats are now starting to be monitored worldwide (Halpern *et al.*, 2019; Jouffray *et al.*, 2020), the mechanisms through which they impact marine systems remain largely unknown (Gissi *et al.*, 2021). As the unprecedented loss in marine biodiversity and resulting ecosystem disruptions (Jones *et al.*, 2018; IPBES, 2019) threaten the global ocean health (Bindoff *et al.*, 2019; IPCC, 2022), a multidimensional understanding of the underlying ecological processes involved from pressure exposure to ecological response is urgently needed. In this regard, flows within and among ecosystems, whether at sea or at the land–sea interface, largely support the functioning and global productivity of the ocean (Ward *et al.*, 2020; Beger *et al.*, 2022). They include abiotic horizontal and vertical flows of nutrients, materials and detritus, which drive marine food-web productivity (Chavez & Messié, 2009; Chassot *et al.*, 2010; Hagen *et al.*, 2012), but also the many spatial flows of compounds, matter and energy associated with the movements of marine organisms. These latter shape local ecosystem dynamics and productivity (Massol *et al.*, 2017; Cannizzo *et al.*, 2021) by controlling food-web structure (Gravel *et al.*, 2011) and modulating ecosystem functioning and resilience through changes in community composition (Guzman *et al.*, 2019; Gladstone-Gallagher *et al.*, 2019) and biodiversity (Fontoura *et al.*, 2022). Although ecosystem functioning results from the combined influence of structural and functional connectivity, recent studies showing a positive link between the stability of several marine ecosystems' functions and local biodiversity (e.g. Brandl *et al.*, 2019; Gonzalez *et al.*, 2020) confirmed that the global Biodiversity–Ecosystem Function (BEF) relationship (Naeem *et al.*, 1994; Gonzalez *et al.*, 2020) also applies at sea. As biologically mediated functions in marine ecosystems largely control biogeochemical cycling (Martinelli & Augusto, 2022), changes in marine species distribution and movements also regulate nutrient cycling and sequestration, with implications for overall planetary functioning (Doughty *et al.*, 2016). These findings call for rapid identification of general trends in MFC and their drivers better to anticipate biodiversity and ecosystem responses to global change and predict the future evolution of connectivity in the ocean and at the land–sea interface. This is a challenging task because MFC operates both within ecosystems (e.g. among habitat patches or depths) and across them, through exchanges among metapopulation, metacommunity, and meta-ecosystem networks. Moreover, connectivity is neither constant nor static: it varies across regions and systems (Martensen *et al.*, 2017) and changes over time in complex ways, as modifications in biodiversity structure affect the contribution of connectivity to ecosystem functioning, and *vice versa* (Gonzalez *et al.*, 2020). The rapid pace of current environmental changes further complicates the situation (Cannizzo *et al.*, 2021). For example, climate change alters ocean temperature, hydrodynamics, and water chemistry (Caesar *et al.*, 2021), but also the distribution, physiology, biology, ethology, and ecology of marine organisms (Lenoir *et al.*, 2020). These changes directly affect connectivity, altering migrations, larval dispersal, and other life-cycle processes, leading to unexpected community shifts that can jeopardize ecosystem functioning (Gerber *et al.*, 2014; Cannizzo *et al.*, 2021; Worm & Lotze, 2021).

Achieving a comprehensive understanding of the role of MFC in biosphere functioning and evolution therefore necessitates integrating multiple knowledge and value systems, transdisciplinary research spanning local to global scales, and supporting data and analytical tools. A critical first step is to standardize terminologies and concepts of connectivity across marine environmental research disciplines so that their work on MFC patterns, drivers and evolutionary, ecological, and socio-economic consequences can be better integrated (see Section III). For example, many important ecosystem processes, like dispersal, nutrient subsidies, gene flow, species invasions, and disease spread, are commonly described under the banner of connectivity research, but the available data and ecological understanding are often inadequate for multiscale quantification and conservation planning (Cumming *et al.*, 2022). New MFC knowledge is also required to address unanswered connectivity questions (Darnaude *et al.*, 2022; Tanner *et al.*, 2025). Research priorities in this regard include a holistic, transboundary assessment of MFC along an inshore–coastal–offshore gradient, from continental rivers to the deep seas, to quantify interdependencies between coastal and pelagic systems and across the land–sea interface. In this regard, targeted efforts are urgently required to assess the extent and relative importance of human-driven dispersal of marine species and its impacts on community composition and ecosystem functioning (Bullock *et al.*, 2018; Donelan *et al.*, 2022). Similarly, defining shared ecoscapes in all oceans and seas to facilitate the movement of obligate range-shifting species is critical to mitigate the negative impacts of global change (Keeley, Beier & Jenness, 2021). Lastly, more research is urgently needed to link MFC directly to ecosystem processes, and upscale connectivity research from species to function (Wood *et al.*, 2022). For this, new integrative estimates of lifetime and transgenerational connectivity are required at the guild and community level. Different connectivity subcategories that have thus far been largely studied separately (e.g. 'genetic', 'ontogenetic', and 'trophic' connectivity) must also be integrated to upscale MFC studies from species or population levels to biologically mediated ecosystem functions and services. Multiplying transdisciplinary interactions to improve MFC data integration into spatial ecological modelling – for example, in metapopulation, metacommunity and meta-ecosystems models – shows great promise (Warmuth *et al.*, 2025). Recent methodological developments in functional ecology linking individual movements and trait expression to ecosystem properties and processes (e.g. Martensen *et al.*, 2017; Villarino *et al.*, 2018; Fontoura *et al.*, 2022; Wood *et al.*, 2022) also pave the way for such integration. Further momentum in this area will be key to adequately quantifying past and future changes in MFC patterns and inferring their ecological and evolutionary consequences.

(3) Providing relevant MFC data and decision-making tools

Marine resources represent some of the world's largest economic assets, and their value is projected to double by 2030 (Sumaila *et al.*, 2021). Nevertheless, given the spatio-temporal heterogeneity across marine habitats, and increasing human impacts (Halpern *et al.*, 2019; Jouffray *et al.*, 2020), the development of a sustainable ocean economy requires informed decisions on where, when, and how to exploit, conserve or restore marine species and ecosystems (Darnaude *et al.*, 2022). For this, leveraging MFC knowledge and understanding is key. By facilitating range shifts of native species and supporting species and ecosystem adaptations in the face of environmental change (Berumen *et al.*, 2012; Bernhardt & Leslie, 2013), establishing well-connected and ecologically coherent protected area networks and other effective area-based conservation measures (OECMs) can provide scalable solutions to many environmental, social and economic challenges (Hilty *et al.*, 2020). Therefore, applying MFC knowledge can greatly improve global, regional, and national plans for biodiversity conservation, climate change adaptation, and environmental sustainability (Hilty *et al.*, 2020; Hartfelder *et al.*, 2020). Yet, despite recent efforts to incorporate ecological connectivity into the design of MPA networks (e.g. Arafeh-Dalmau *et al.*, 2017; Lett *et al.*, 2024; Blouet *et al.*, 2025), this goal remains largely unmet, as conservation, planning and legislation have thus far overlooked the ecological processes that underpin the long-term viability of species assemblages (Magris *et al.*, 2014; Gardner *et al.*, 2024). Ocean governance has long focused on conserving ecologically important areas, but connectivity among these often-isolated pockets has often been neglected. Only a handful of recent marine conservation planning applications have included connectivity as an ecological priority, and consideration at the community or ecosystem level is just starting to be implemented (Barnes *et al.*, 2018; Balbar & Metaxas, 2019).

A push towards the co-development of science-based decisions through recognizing the multifaceted value of MFC is needed to drive forward environmental obligations and commitments for marine conservation within and beyond national boundaries (Muller-Karger *et al.*, 2024). However, implementing the protection, maintenance, and restoration of ecological connectivity across different scales requires unprecedented transdisciplinary collaboration among scientists, policymakers, managers, and stakeholders. Developing adequate MFC-informed policies and management strategies demands a shared understanding of local and global knowledge needs, goals, and possible actions, particularly with respect to the evolutionary and ecological consequences of connectivity. Again, a major obstacle is the lack of consistency between working definitions and quantification methods in connectivity science (LaPoint *et al.*, 2015). This complicates communication between scientists and stakeholders, hinders awareness among decision-makers of the inherent value of integrating connectivity data (Bryan-Brown *et al.*, 2017; Balbar & Metaxas, 2019), and complicates bridging gaps in understanding connectivity processes that are critical for sustainable marine management, such as self-recruitment and life-cycle diversity in marine populations (Bradbury *et al.*, 2008; Jones *et al.*, 2009; Riginos *et al.*, 2014). However, the application of MFC knowledge in marine policy and management is also hampered by a marked lack of appropriate decision-making tools and governance or management frameworks. Given the cross-jurisdictional nature of marine ecosystems and the diversity of transboundary processes shaping connectivity, significant advances in international cooperation are required to overcome complications from sovereignty, political status, and international law issues (Mackelworth *et al.*, 2019; Teff-Seker *et al.*, 2020). Moreover, MFC is not a static attribute of ecosystems or species, but rather one that evolves constantly in line with environmental changes, which are currently prone to accelerate (Halpern *et al.*, 2019; Jouffray *et al.*, 2020). To be effective, therefore, MFC-informed management and policy will have to be adaptive and based on complex and specific connectivity metrics or models which are only in their infancy (Darnaude *et al.*, 2024).

III. A GLOBAL CONCEPTUAL FRAMEWORK TO UNIFY MFC RESEARCH

Addressing the challenges outlined above requires progress towards a more coherent global approach to monitoring and conserving ecological connectivity, integrating MFC-focused research fields and the different data they provide and facilitating global MFC knowledge uptake by scientists and decision-makers. A critical first step is to remove the confusion surrounding the MFC concept and the forms of connectivity it encompasses. This will catalyse data sharing and research integration between the complementary scientific disciplines that measure or predict the distribution and movements of marine organisms, but also across the disciplines that infer the drivers and predict the consequences of MFC or apply this knowledge in management and conservation settings.

(1) Refining connectivity definitions and subcategories

In ecology, 'connectivity' was initially used to describe food-web configuration (Kercher & Shugart, 1975) and was only first applied in the mid-1980s to describe spatial connections and their ecological consequences (Merriam, 1984; Fahrig & Merriam, 1985). Since then, many researchers have tried to clarify the ecological meaning of the term and the variety of fluxes it encompasses (e.g. Hillman *et al.*, 2018; Hilty *et al.*, 2020; Beger *et al.*, 2022). Until the early 2000s, general definitions of connectivity in marine ecology centred on among-population exchanges of eggs, larvae, juveniles or adults, with a focus on gene flow (e.g. Palumbi, 2003; Cowen, Paris & Srinivasan, 2006). The concept has since progressively included other elements of ecosystem functioning, such as nutrients, organic and inorganic materials (e.g. Cowen & Sponaugle, 2009; Auffret *et al.*, 2015), and finally energy, processes and disturbance (e.g. Carr *et al.*, 2017; Hillman *et al.*, 2018; Beger *et al.*, 2022). Recent papers (Table 1) often propose very broad definitions for '(ecological spatial) connectivity', referring to all the unimpeded flows of organisms, non-living material, and natural processes (including energy and disturbance effects) that occur between ecosystems and are essential for the persistence of wild populations and communities (e.g. Hilty *et al.*, 2020; Cannizzo *et al.*, 2021; Hilliam, Floerl & Treml, 2024). However, considerable variation between definitions in recent marine literature still persists (Table 1). While the broad concept of ecological connectivity is sometimes referred to as 'ecosystem connectivity' (e.g. Carr *et al.*, 2017) or 'ecosystem process connectivity' (e.g. Hillman *et al.*, 2018), to reflect its comprehensive nature, other studies still use ecological connectivity to refer uniquely to species' movements (e.g. Hartfelder *et al.*, 2020; Wood *et al.*, 2022). In both cases, the definitions focus either on the nature of the exchanges (e.g. Olds *et al.*, 2016; Hilty *et al.*, 2020; Berkström, Wennerström & Bergström, 2022), often interchangeably referred to as 'movements', 'links', 'flows' or 'fluxes', or on the role of the landscape or seascape in limiting or facilitating such exchanges (e.g. Bishop *et al.*, 2017; Wood *et al.*, 2022). Finally, while some authors consider marine connectivity as a general property of the seascape (e.g. Bishop *et al.*, 2017; Balbar & Metaxas, 2019), others frame it as the ecological process connecting discrete

Table 1. Examples of the diversity of subcategories, definitions and terminology for ecological connectivity in recent literature.

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
General ecological connectivity	Connectivity	Beger *et al.* (2022)	Both (theoretical)	Theory in spatial conservation science and planning	'The flow of energy, materials, and organisms across space'.	Structural *vs* Functional Connectivity; Genetic *vs* Ontogenetic Connectivity; Temporal Connectivity	**Movement**, **dispersal**, **migration**, **flow**, spread, shift, **network**, **patches**, subsidies, **corridor**, **linkages**, distance, pathway, patterns, connections, spatial dependencies, **metapopulation**, metacommunity.
	Connectivity	Olds *et al.* (2018)	Marine	Theory in ecology	'The movements of organisms, energy and nutrients that link populations, habitats, food webs and ecosystems across the boundaries of seascapes and landscapes'.	Potential *vs* Actual *vs* Structural Connectivity; Population *vs* Habitat *vs* Ecosystem *vs* Seascape Connectivity; Genetic *vs* Trophic *vs* Functional *vs* Ontogenetic Connectivity	**Movement**, **dispersal**, **migration**, **isolation**, transfer, relay, spread, spillover, network, patches, subsidy, links, **linkages**, **connections**, barriers, **boundaries**.
	Connectivity	Selkoe *et al.* (2016)	Marine	Theory and applications in seascape genetics	'Any relationship between spatially or temporally distinct entities'.	Structural *vs* Functional Connectivity; Demographic *vs* Genetic Connectivity; Adaptative Genetic *vs* Neutral Genetic Connectivity	Movement, **dispersal**, **migration**, **transport**, **colonization**, **flow**, **exchange**, **isolation**, retention, self-recruitment, shift, network, patches, links, **boundaries**, **isolation**, source–sink, **metapopulation**, range.
	Connectivity	Auffret *et al.* (2015)	Mainly continental (theoretical)	Theory in ecology	'How the movement of various ecological units or entities is facilitated by their surroundings'.	Structural *vs* Functional Connectivity	**Movement**, **dispersal**, migration, colonization, flow, isolation, network, patches, **fragmentation**, metapopulation.
	Connectivity	Hartfelder *et al.* (2020)	Mainly continental (theoretical)	Theory & modelling in ecology	'The degree to which individuals can move across landscapes'.	–	**Movement**, **dispersal**, isolation, **network**, **patches**, **linkages**, **distance**, **metapopulation**.
	Ecological connectivity	Cramer *et al.* (2023)	Mainly marine (theoretical)	Theory in conservation science	'The movements of species and the flow of natural processes that sustain life on Earth'.	Structural *vs* Functional Connectivity; Population Ecological *vs* Population Evolutionary Connectivity; Demographic *vs* Genetic Connectivity	**Movement**, **dispersal**, **migration**, **flow**, flux, isolation, patch(es), corridor, **connections**, **interactions**, **metapopulation**, **subpopulations**, population structure, **range**.

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
	Ecological connectivity	Hilty *et al.* (2020)	Both	Guidance for management & policy in conservation science	'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'.	Structural *vs* Functional Connectivity	**Movement**, **dispersal**, **migration**, **flow**, **spread**, **range shift**, **exchange**, **network**, **patches**, **corridor**, **links**, **linkages**, **distance**, pathways, **patterns**, **fragmentation**, barriers, **stepping stones**, metapopulation, subpopulations.
	Ecological connectivity	Cannizzo *et al.* (2021)	Marine	Advancing MPA management	'The unimpeded movement of species and the flow of natural processes that sustain life on Earth. This includes the movement of populations, and that of individuals, genes, gametes, and propagules between populations, communities, and ecosystems, as well as that of non-living material from one location to another and the connectivity that is inherently present in large wild areas'.	Structural *vs* Functional Connectivity, Passive (Oceanographic) *vs* Active (Migratory) Connectivity, Habitat Connectivity, Seascape Connectivity	**Movement**, **dispersal**, migration, flow, shift, **network**, patches, **corridor**, stepping stones, **linkage(s)**, connections.
	Ecological connectivity	Bishop *et al.* (2017)	Marine	Marine environmental science	'The way in which the landscape facilitates or impedes the movement of organisms, materials and energy between habitat unit'.	Structural *vs* Functional Connectivity, Trophic Connectivity	**Movement**, **dispersal**, **migration**, **transport**, **flow**, **spread**, spillover, shift, expansion, **patches**, **subsidies**, **corridors**, pathways, patterns, interactions, **barriers**, **boundaries**, fragmentation, **stepping stones**, **source**, sink, metapopulation, range.
	Ecological connectivity	Wood *et al.* (2022)	Mainly continental (theoretical)	Modelling in ecology	'Measures the extent to which a landscape facilitates or impedes species movement'.	Individual-species *vs* Multi-species Connectivity; Functional Connectivity, Genetic Connectivity	**Movement**, **dispersal**, colonization, **flow**, **network**, **patches**, **corridors**, **link(s)**, linkages, pathways, patterns, distance(s), **fragmentation**, **metapopulation**, metacommunity.
	Ecological connectivity	Saunders *et al.* (2016)	Both (marine and freshwater)	Modelling in ecology	'The exchange of individuals among habitat patches or subpopulations in metapopulations'.	Structural *vs* Hydrologic *vs* Functional Connectivity; Landscape Connectivity	**Movement**, **dispersal**, **migration**, **network**, patches, corridor, **links**, **linkages**, connections, pathways, **patterns**, **distance**, boundaries, fragmentation, **metapopulation**, subpopulations, **range**.

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
	(Ecological spatial) connectivity	Balbar & Metaxas (2019)	Marine	MPA design and management	'The extent to which spatially distinct populations, communities, ecosystems, or habitats are linked by the exchange of genes, organisms (propagules, juveniles and adults), nutrients and energy.'	Structural *vs* Functional Connectivity; Landscape Connectivity; Population *vs* Community *vs* Ecosystem Connectivity; Genetic *vs* Demographic Connectivity	**Movement**, **dispersal**, migration, **flow**, transport, exchange, **retention**, spillover, self-recruitment, **network**, patches, corridors, linkages, **connections**, **distance**, barriers, **source**, sink, self-replenishing population, **metapopulation**, population structure, home range.
	Ecological spatial connectivity	Carr *et al.* (2017)	Marine	MPA management in conservation Science	'The processes by which genes, organisms, populations, species, nutrients, and/or energy move among spatially distinct habitats, populations, communities, or ecosystems'.	Population *vs* Genetic *vs* Community *vs* Ecosystem Connectivity	**Movement**, **dispersal**, **migration**, gene flow, **shift**, spillover, **network**, subsidies, corridor, linkage(s), connections, **interactions**, **distance**, **source**, sink, **metapopulation**, metacommunity(ies), subpopulation, **range**.
	Ecological spatial connectivity	Berkström *et al.* (2022)	Marine	MPA design and management	'Movement and dispersal of eggs, spores, larvae and older individuals among spatially distinct entities'	Passive *vs* Active Connectivity; Genetic Connectivity	**Movement**, **dispersal**, **migration**, **flow**, exchange, **network**, patches, corridors, **distance**, **barriers**, **home range**.
	Ecoscape (or ecosystem) connectivity	Keeley *et al.* (2022)	Both (marine and freshwater)	Ecosystem management (conservation & policy science)	'The merger of connectivity concepts across systems and scales'.	Longitudinal *vs* Vertical *vs* Lateral Connectivity; Lattice Connectivity; Teleconnectivity; Hydrological Connectivity; Social Connectivity	**Movement**, dispersal, **migration**, **transport**, **flow**, **exchange**, shift, **network**, patches, **corridors**, links, connections, distance, barriers, boundaries, fragmentation, stepping stones, range.
	Ecosystem (process) connectivity	Hillman *et al.* (2018)	Both	Theory & management in conservation science	'Includes population dynamics in heterogeneous environments but also how resources are moved, transformed or stored within and between habitats, including the fluxes and sinks in energy, nutrients, and the propagation of disturbance effects'.	Population *vs* Ecosystem (Process-based) Connectivity; Demographic *vs* Functional *vs* Neutral Genetic Connectivity; Habitat connectivity	**Movement**, **dispersal**, transport, **flow**, **flux**, exchange, **patches**, subsidies, linkages, **connections**, **fragmentation**, **source**, **sink**, metapopulations, **meta-ecosystems**.

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
	Ecosystem connectivity	Carr *et al.* (2017)	Marine	MPA management in conservation science	'The most complex type of ecological spatial connectivity, resulting from the movement of multiple species among distinct ecological communities, along with the movement of chemicals (e.g. nutrients and pollutants), energy (in the form of organisms), and materials (e.g. sediments and debris)'.	–	**Movement**, **dispersal**, **migration**, gene flow, **shift**, spillover, **network**, subsidies, corridor, linkage(s), connections, **interactions**, **distance**, **source**, sink, **metapopulation**, metacommunity(ies), subpopulation, **range**.
Potential connectivity	Potential connectivity	Olds *et al.* (2018)	Marine	Theory in seascape ecology	'Inferred from distribution and spatial properties of seascapes, with some data on mobility'.	–	**Movement**, **dispersal**, **migration**, **isolation**, transfer, relay, spread, spillover, network, patches, subsidy, links, **linkages**, **connections**, barriers, **boundaries**.
	Potential connectivity	Fletcher *et al.* (2016)	Mainly continental (theoretical)	Theory in landscape ecology	'Combined attributes of landscape configuration with information on the assumed dispersal or movement distances to predict linkages'.	–	**Movement**, **dispersal**, (im−/e-) **migration**, **flow**, spread, range expansion, habitat use, **network**, **patches**, corridors, **linkages**, **path**, **distance**, boundaries, fragmentation, isolation, **metapopulation**, **metacommunities**, subpopulations, population/genetic structure
Actual (or Realized) connectivity	Actual connectivity	Olds *et al.* (2018)	Marine	Theory in ecology	'Connectivity measured directly'.	–	**Movement**, **dispersal**, **migration**, **isolation**, transfer, relay, spread, spillover, network, patches, subsidy, links, **linkages**, **connections**, barriers, **boundaries**.
	Realized connectivity	Matos *et al.* (2024)	Marine	Modelling in conservation science	'The actual population connectivity patterns which result from the transference of individuals and genetic material among sub-populations'.	–	**Dispersal**, migration, **exchange(s)**, **retention**, **network**, patches, **links**, **connections**, **pathways**, **patterns**, **distance**, isolation, **source**, sink, stepping stone.

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
	Realized connectivity	Fletcher *et al.* (2016)	Mainly continental (theoretical)	Theory in landscape ecology	'Directly measuring the realized flow and/or movement of organisms to estimate the linkages between patch or landscape elements'.	–	**Movement**, **dispersal**, (im−/e-) **migration**, **flow**, spread, range expansion, habitat use, **network**, **patches**, corridors, **linkages**, **path**, **distance**, boundaries, fragmentation, isolation, **metapopulation**, **metacommunities**, subpopulations, population/genetic structure.
Landscape/ Seascape connectivity	Landscape connectivity	Hartfelder *et al.* (2020)	Mainly continental (theoretical)	Theory & modelling in landscape ecology	'The interplay of organismal movement with the structure of the landscape'.	–	**Movement**, **dispersal**, isolation, **network**, **patches**, **linkages**, **distance**, **metapopulation**.
	Landscape connectivity	Mony *et al.* (2022)	Both	Micro-organism ecology	'The degree to which the landscape facilitates or impedes movement between habitat patches'.	Non-biotic *vs* Biotic (host or vector) Connectivity; Structural *vs* Functional Connectivity; Micro-Connectivity	**Movement**, **dispersal**, migration, flow, fluxes, spillover, **colonization**, network, **patches**, **corridors**, pathways, patterns, **distance**, boundaries, **fragmentation**, **isolation**, metapopulation, **metacommunity(ies)**.
	Seascape connectivity	Olds *et al.* (2016)	Marine	Guidance for management & policy in conservation science	'Physical linkages between discontinuous habitats (either of the same or of different types) of the seafloor'.	Structural *vs* Functional Connectivity	**Movement**, **dispersal**, migration, isolation, spread, **spillover**, shift, **network**, **patches**, **linkages**, connections, distance, **boundaries**.
	Seascape connectivity	Peterson *et al.* (2024)	Marine	Modelling marine connectivity hotspots	'How the spatial configuration of marine habitats facilitates or hinders the movement of organisms, nutrients, materials or energy'.	Structural *vs* Functional Connectivity; Local *vs* Global (network level) Connectivity	**Movement**, flow, **flux(es)**, habitat use, **network**, **patches**, corridor, linkages, **distance**, patterns, **pathways**, home range.
	Seascape connectivity	Pittman *et al.* (2021)	Marine	Theory in ecology	'The degree to which a seascape facilitates or hinders the movement of organisms, or the flow of genetic material, nutrients, and other matter'.	Actual *vs* Potential Connectivity; Horizontal *vs* Vertical Connectivity; Structural Connectivity	**Movement**, dispersal, migration, **flow**, **network**, **patches**, **corridor**, **linkages**, connections, pathways, **patterns**, boundaries, **fragmentation**, metapopulation, range.
	Seascape connectivity	Cannizzo *et al.* (2021)	Marine	Advancing MPA management	'The linkage between habitats of differing types'.	–	**Movement**, **dispersal**, migration, flow, shift, **network**, patches, **corridor**, stepping stones, **linkage(s)**, connections.

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
Structural connectivity	Structural connectivity	Hilty *et al.* (2020)	Both	Guidance for management and policy in conservation science	'A measure of habitat permeability based on the physical features and arrangements of habitat patches, disturbances and other land, freshwater or seascape elements presumed to be important for organisms to move through their environment'.	–	**Movement**, **dispersal**, **migration**, **flow**, **spread**, **range shift**, **exchange**, **network**, **patches**, **corridor**, **links**, **linkages**, **distance**, pathways, **patterns**, **fragmentation**, barriers, **stepping stones**, metapopulation, subpopulations.
	Structural connectivity	Beger *et al.* (2022)	Both (theoretical)	Theory in spatial conservation science and planning	'Habitat or physical features or processes that may form a platform for the movement of agents (organisms, pollutants, pathogens)'.	–	**Movement**, **dispersal**, **migration**, **flow**, spread, shift, **network**, **patches**, subsidies, **corridor**, **linkages**, distance, pathway, patterns, connections, spatial dependencies, **metapopulation**, metacommunity.
	Structural connectivity	Selkoe *et al.* (2016)	Marine	Theory and applications in seascape genetics	'The physical relationships of landscape elements, including spatial positioning of habitat'.	–	Movement, **dispersal**, **migration**, **transport**, **colonization**, **flow**, **exchange**, **isolation**, retention, self-recruitment, shift, network, patches, links, **boundaries**, **isolation**, source–sink, **metapopulation**, range.
	Structural connectivity	Auffret *et al.* (2015)	Mainly continental (theoretical)	Theory in ecology	'A general measure of connectivity related to the physical characteristics of the landscape, without any consideration of the attributes of any potential organisms'.	–	**Movement**, **dispersal**, migration, colonization, flow, isolation, network, patches, **fragmentation**, metapopulation.
	Structural connectivity	Matos *et al.* (2024)	Marine	Modelling in conservation science	'Often referred as "connectedness", it incorporates only information about the physical attributes of the landscape (e.g. habitat location, size, and shape) and refers to the physical links between their elements'.	–	**Dispersal**, migration, **exchange(s)**, **retention**, **network**, patches, **links**, **connections**, **pathways**, **patterns**, **distance**, isolation, **source**, sink, stepping stone.

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Table 1. *(Cont.)*

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	Structural connectivity	Bishop *et al.* (2017)	Marine	Marine environmental science	'The configuration of the landscape and habitat patches'.	–	**Movement**, **dispersal**, **migration**, **transport**, **flow**, **spread**, spillover, shift, expansion, **patches**, **subsidies**, **corridors**, pathways, patterns, interactions, **barriers**, **boundaries**, fragmentation, **stepping stones**, **source**, sink, metapopulation, range.
	Structural connectivity	Olds *et al.* (2018)	Marine	Theory in seascape ecology	'Connectivity inferred from distribution and spatial properties of seascapes'.	–	**Movement**, **dispersal**, **migration**, **isolation**, transfer, relay, spread, spillover, network, patches, subsidy, links, **linkages**, **connections**, barriers, **boundaries**.
Hydrological connectivity	Hydrological connectivity	Keeley *et al.* (2022)	Both (marine and freshwater)	Ecosystem management (conservation & policy science)	'The water mediated transfer of matter, energy, and organisms within or between elements of the hydrological cycle'.	–	**Movement**, dispersal, **migration**, **transport**, **flow**, **exchange**, shift, **network**, patches, **corridors**, links, connections, distance, barriers, boundaries, fragmentation, stepping stones, range.
	Hydrologic connectivity	Saunders *et al.* (2016)	Both (marine and freshwater)	Modelling in ecology (conservation science)	'The advection and diffusion of water in aquatic environments'.	–	**Movement**, **dispersal**, **migration**, **network**, patches, corridor, **links**, **linkages**, connections, pathways, **patterns**, **distance**, boundaries, fragmentation, **metapopulation**, subpopulations, **range**.
Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
Functional (Biological) connectivity	Functional connectivity	Beger *et al.* (2022)	Both (theoretical)	Theory in spatial conservation science and planning	'The effective movement of agents across a structurally connected ecosystem, such as dynamic flows of matter and energy'.	Ontogenetic *vs* Dispersal Connectivity	**Movement**, **dispersal**, **migration**, **flow**, spread, shift, **network**, **patches**, subsidies, **corridor**, **linkages**, distance, pathway, patterns, connections, spatial dependencies, **metapopulation**, metacommunity.
	Functional Connectivity	Hilty *et al.* (2020)	Both	Guidance for management and policy in conservation science	'A description of how well genes, gametes, propagules or individuals move through land- and seascape'.	–	**Movement**, **dispersal**, **migration**, **flow**, **spread**, **range shift**, **exchange**, **network**, **patches**, **corridor**, **links**, **linkages**, **distance**, pathways, **patterns**, **fragmentation**,

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
							barriers, **stepping stones**, metapopulation, subpopulations.
	Functional connectivity	Saunders *et al.* (2016)	Both (marine and freshwater)	Modelling in ecology	'The morphological, behavioural and ontogenetic characteristics affecting movement and dispersal of organisms'.	–	**Movement**, **dispersal**, **migration**, **network**, patches, corridor, **links**, **linkages**, connections, pathways, **patterns**, **distance**, boundaries, fragmentation, **metapopulation**, subpopulations, **range**.
	Functional connectivity	Selkoe *et al.* (2016)	Marine	Theory and applications in seascape genetics	'The patterns and rates of dispersal that result from the response of individuals to the structural matrix, mediated by behavioral traits and dispersal success'.	Demographic *vs* Genetic Connectivity; Adaptative Genetic *vs* Neutral Genetic Connectivity	Movement, **dispersal**, **migration**, **transport**, **colonization**, **flow**, **exchange**, **isolation**, retention, self-recruitment, shift, network, patches, links, **boundaries**, **isolation**, source–sink, **metapopulation**, range.
	Functional connectivity	Auffret *et al.* (2015)	Mainly continental (theoretical)	Theory in ecology (conservation science)	'The behavioural responses of an organism to the various landscape elements, referring to the actual flow of individuals and their genes among habitat patches'.	Spatial (movement in space) *vs* temporal (persistence in time) functional connectivity	**Movement**, **dispersal**, migration, colonization, flow, isolation, network, patches, **fragmentation**, metapopulation.
	Functional connectivity	Peterson *et al.* (2024)	Marine	Modelling marine connectivity hotspots	'How structural patterns influence the movement of animals, as well as their energy, nutrients, genetic material and ecological functions'.	Potential *vs* Realized Connectivity; Species-specific Connectivity	**Movement**, flow, **flux (es)**, habitat use, **network**, **patches**, corridor, linkages, **distance**, patterns, **pathways**, home range.
	Functional connectivity	Olds *et al.* (2016)	Marine	Guidance for management and policy in conservation science	'The movement of organisms (and the organic matter derived from them) through the ocean, as a result of their ecological characteristics, such as habitat preference and dispersal ability'.	–	**Movement**, **dispersal**, migration, isolation, spread, **spillover**, shift, **network**, **patches**, **linkages**, connections, distance, **boundaries**.
	Functional connectivity	Allgayer *et al.* (2024)	Marine	Modelling in fishery science	'Considers how individuals move within the environment, taking into	–	**Movement**, **dispersal**, **migration**, **colonisation**,

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
					account species-specific traits'.		**transport**, **exchange**, mixing, shift, **self-recruitment**, **network**, **patches**, connections, **distance**, boundaries, **isolation**, source, **metapopulation**, **subpopulation(s)**, range.
	Functional connectivity	Pittman *et al.* (2018)	Marine	Theory and applications in seascape ecology	'The movement response of organisms to various structural features of the landscape'.	Potential *vs* Actual Connectivity; Population Connectivity; Demographic *vs* Genetic (or Evolutionary) Connectivity	**Movement**, dispersal, migration, flow, habitat use, **network**, **patches**, **corridors**, linkages, **pathways**, **patterns**, distance, barriers, **boundaries**, fragmentation, **range**.
	Functional connectivity	Olds *et al.* (2018)	Marine	Theory in seascape ecology (conservation science)	'Spatial effects of one ecosystem on ecological functions in another'.	–	**Movement**, **dispersal**, **migration**, **isolation**, transfer, relay, spread, spillover, network, patches, subsidy, links, **linkages**, **connections**, barriers, **boundaries**.
	Functional connectivity	Bishop *et al.* (2017)	Marine	Marine environmental science	'The response of organisms or particles to the landscape'.	–	**Movement**, **dispersal**, **migration**, **transport**, **flow**, **spread**, spillover, shift, expansion, **patches**, **subsidies**, **corridors**, pathways, patterns, interactions, **barriers**, **boundaries**, fragmentation, **stepping stones**, **source**, sink, metapopulation, range.
	Functional connectivity	Hidalgo *et al.* (2017)	Marine	Marine environmental science	'Influence of connectivity processes on ecological function and ecosystems services'.	Demographic *vs* Evolutionary/ genetic Connectivity	**Movement**, **dispersal**, migration, transport, flow, exchange, mixing, retention, network, pathways, **patterns**, distance, boundaries, source, metapopulation, population structure.
	Population connectivity	Cramer *et al.* (2023)	Mainly marine (theoretical)	Theory in conservation science	'The relationship between populations or groups of organisms, encompassing their direct and indirect	Population Ecological *vs* Population Evolutionary Connectivity; Demographic *vs* Genetic Connectivity	**Movement**, **dispersal**, **migration**, **gene flow**, isolation, patch(es), corridor, **connections**,

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
					interactions, encompassing the movement of individuals between groups or species, the flow of genes between groups, or even indirect interactions between groups across a landscape'.		**interactions**, **metapopulation**, **population structure**, **subpopulations**, range.
	Population connectivity	Treml & Kool (2018)	Marine	Theory and applications in seascape ecology	'The biophysical functional relationships or the likelihood of individual movement among subpopulations over several generations, or gene flow over the last millennia'.	Potential *vs* Actual Connectivity; Demographic *vs* Genetic (Evolutionary) Connectivity	**Movement**, **dispersal**, **migration**, transport, **flow**, fluxes, **spread**, **retention**, **network**, **patches**, corridors, **links**, **linkages**, **connections**, **pathways**, **patterns**, **distance**, isolation, **source**, **sink**, metapopulation, **subpopulations**.
	Population (Demographic) connectivity	Carr *et al.* (2017)	Marine	MPA management in conservation science	'Results from the movement of individuals of a single species among patchily distributed local or subpopulations'.	–	**Movement**, **dispersal**, **migration**, gene flow, **shift**, spillover, **network**, subsidies, corridor, linkage(s), connections, **interactions**, **distance**, **source**, sink, **metapopulation**, metacommunity(ies), subpopulation, **range**.
	Community connectivity	Carr *et al.* (2017)	Marine	MPA management in Conservation science	'The linkage of spatially separated ecological communities resulting from the movements of multiple species among these areas in ways that affect their species composition and ecological structure and processes'.	–	**Movement**, **dispersal**, **migration**, gene flow, **shift**, spillover, **network**, subsidies, corridor, linkage(s), connections, **interactions**, **distance**, **source**, sink, **metapopulation**, metacommunity(ies), subpopulation, **range**.
	Multi-species connectivity	Wood *et al.* (2022)	Mainly continental (theoretical)	Modelling in ecology (conservation science)	'A network of habitats and movement pathways that supports the long-term persistence of multiple species in a landscape'.	–	**Movement**, **dispersal**, colonization, **flow**, **network**, **patches**, **corridors**, **link(s)**, linkages, pathways, patterns, distance(s),

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
							fragmentation, **metapopulation**, metacommunity.
	Biological connectivity	Villarino *et al.* (2018)	Marine	Plankton composition and connectivity	'The exchange of individuals across geographically separated subpopulations'.	–	Movement, **dispersal**, migration, transport, network, **patches**, connections, pathways, **distance**, barriers, geographic range.
Active (Migratory) connectivity	Active connectivity	Johansen *et al.* (2021)	Marine	Connectivity integration in the Law of the Sea	'The migration of marine species and marine organisms, and more specifically the movement of marine animals across the ocean and up and down through the water column'.	–	**Movement**, dispersal, **(inter)linkages**, boundaries, fragmentation.
	Active (Migratory) connectivity	Cannizzo *et al.* (2021)	Marine	Advancing MPA management	'The purposeful, self-directed movement of organisms from place to place'.	–	**Movement**, **dispersal**, migration, flow, shift, **network**, patches, **corridor**, stepping stones, **linkage(s)**, connections.
	Migratory connectivity	McMahon *et al.* (2013)	Both (marine and freshwater)	Chemical markers to study connectivity	'Refers to movement of individuals between locations due to shifts in some key resource, such as food availability or breeding requirements, often on seasonal time scales'.	–	**Movement**, **dispersal**, **migration**, **habitat use**, linkages, pathways, **patterns**, isolation.
Passive connectivity	Passive (Oceanographic) connectivity	Johansen *et al.* (2021)	Marine	Connectivity integration in the Law of the Sea	'The transportation of material such as nutrients, small marine organisms and other marine organisms by ocean currents and processes such as sinking and upwelling'.	–	**Movement**, dispersal, **(inter)linkages**, boundaries, fragmentation.
	Passive (Oceanographic) connectivity	Cannizzo *et al.* (2021)	Marine	Advancing MPA management	'The incidental movement of organisms, nutrients, and materials through physical processes such as currents, sinking, or upwelling'.	–	**Movement**, **dispersal**, migration, flow, shift, **network**, patches, **corridor**, stepping stones, **linkage(s)**, connections.
	Non-Biotic connectivity (for micro-organisms)	Mony *et al.* (2022)	Both	Micro-organism ecology	'The degree to which the abiotic landscape facilitates or prevents movement, and especially	–	**Movement**, **dispersal**, migration, flow, fluxes, spillover, **colonization**, network, **patches**,

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
					dispersal movements, among habitat patches'.		**corridors**, pathways, patterns, **distance**, boundaries, **fragmentation**, **isolation**, metapopulation, **metacommunity(ies)**.
	Biotic (Host) connectivity (for micro-organisms)	Mony *et al.* (2022)	Both	Micro-organism ecology	'The degree to which the biotic landscape – composed of host(s), either static or mobile – facilitates or prevents movement, and especially dispersal movements, among habitat patches'.	–	**Movement**, **dispersal**, migration, flow, fluxes, spillover, **colonization**, network, **patches**, **corridors**, pathways, patterns, **distance**, boundaries, **fragmentation**, **isolation**, metapopulation, **metacommunity(ies)**.
Transgenerational connectivity	(Population) Evolutionary connectivity	Cramer *et al.* (2023)	Mainly marine (theoretical)	Theory in conservation science	'The gene flow across any timescale'.	Genetic Connectivity	**Movement**, **dispersal**, **migration**, **gene flow**, isolation, patch(es), corridor, **connections**, **interactions**, **metapopulation**, **population structure**, **subpopulations**, range.
	Population connectivity	Hillman *et al.* (2018)	Both	Theory & management in conservation science	'How changes in landscape patterns (i.e., presence, quantity, quality, and configuration of habitat types) influence the exchange of individuals of different life stages, and the possible feedbacks between scale of dispersal and persistence of a population'.	Population Connectivity *vs* Ecosystem (Process-based) Connectivity, Demographic *vs* Functional *vs* Neutral Genetic Connectivity, Habitat connectivity	**Movement**, **dispersal**, transport, **flow**, **flux**, exchange, **patches**, subsidies, linkages, **connections**, **fragmentation**, **source**, **sink**, metapopulations, **meta-ecosystems**.
	Demographic connectivity	Cramer *et al.* (2023)	Mainly marine (theoretical)	Theory in conservation science	'The movement of individuals between geographically different parts of a metapopulation encompassing reproduction at the completion of dispersal'.	–	**Movement**, **dispersal**, **migration**, **gene flow**, isolation, patch(es), corridor, **connections**, **interactions**, **metapopulation**, **population structure**, **subpopulations**, range.

(Continues on next page)

Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
	Demographic connectivity	Manel *et al.* (2019)	Marine	Dispersal from MPAs	'Dispersal of individuals among (sub)populations that survive at the end of the settlement step'.	–	Movement, **dispersal**, migration, gene flow, **spillover**, exchange(s), **network**, patterns, **distance**, **boundaries**, **isolation**, source, sink, **metapopulation**, population structure.
	Demographic connectivity	Selkoe *et al.* (2016)	Marine	Theory and applications in seascape genetics	'Relates the dispersal of individuals to their cumulative effects on population-level processes such as population growth, extinction or recolonization'.	–	Movement, **dispersal**, **migration**, **transport**, **colonization**, **flow**, **exchange**, **isolation**, retention, self-recruitment, shift, network, patches, links, **boundaries**, **isolation**, source–sink, **metapopulation**, range.
	Genetic connectivity	Cramer *et al.* (2023)	Mainly marine (theoretical)	Theory in conservation science	'The degree to which gene flow affects evolutionary processes within populations, dependent on the absolute number of dispersers or percent gene similarity'.	–	**Movement**, **dispersal**, **migration**, **gene flow**, isolation, patch(es), corridor, **connections**, **interactions**, **metapopulation**, **population structure**, **subpopulations**, range.
	Genetic connectivity	Manel *et al.* (2019)	Marine	Dispersal from MPAs	'The exchange of genes among marine populations'.	–	Movement, **dispersal**, migration, gene flow, **spillover**, exchange(s), **network**, patterns, **distance**, **boundaries**, **isolation**, source, sink, **metapopulation**, population structure.
	Genetic connectivity	Carr *et al.* (2017)	Marine	MPA management in Conservation science	'The transfer of genes among populations of a species (also called 'gene flow'), resulting from the movement of organisms – whether spores of marine algae or the larvae, juveniles, or adults of marine animals – among spatially distinct local populations of a single species'.	–	**Movement**, **dispersal**, **migration**, gene flow, **shift**, spillover, **network**, subsidies, corridor, linkage(s), connections, **interactions**, **distance**, **source**, sink, **metapopulation**, metacommunity(ies), subpopulation, **range**.

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
	Genetic connectivity	Selkoe *et al.* (2016)	Marine	Theory and applications in seascape genetics	'Tracks the dispersal of genes (and genomes), which only accounts for those individuals that successfully reproduce after dispersing'.	Adaptative Genetic *vs* Neutral Genetic Connectivity	Movement, **dispersal**, **migration**, **transport**, **colonization**, **flow**, **exchange**, **isolation**, retention, self-recruitment, shift, network, patches, links, **boundaries**, **isolation**, source–sink, **metapopulation**, range.
	Genetic connectivity	Berkström *et al.* (2012)	Marine	Connectivity assessment for MPA network management	'The degree to which gene flow affects evolutionary processes within sub-populations, either directly through dispersal and following establishment and/or reproduction or indirectly by a multi-generational stepping stone process'.	–	**Movement**, **dispersal**, **migration**, exchange, **gene flow**, **network**, patches, corridors, links, **distances**, **patterns**, barrier(s), source populations, **home range(s)**.
	Genetic connectivity	Beger *et al.* (2022)	Both (theoretical)	Theory & application in conservation science	'The movement of genetic material between nearby or distant habitat regions over multiple generations'.	–	**Movement**, **dispersal**, **migration**, **flow**, spread, shift, **network**, **patches**, subsidies, **corridor**, **linkages**, distance, pathway, patterns, connections, spatial dependencies, **metapopulation**, metacommunity.
Lifetime connectivity	Ontogenetic connectivity	Beger *et al.* (2022)	Both (theoretical)	Theory in spatial conservation science & planning	'Movement of individuals occurring as part of life cycles'.	–	**Movement**, **dispersal**, **migration**, **flow**, spread, shift, **network**, **patches**, subsidies, **corridor**, **linkages**, distance, pathway, patterns, connections, spatial dependencies, **metapopulation**, metacommunity.
	Ontogenetic connectivity	Olds *et al.* (2018)	Marine	Theory in seascape ecology	'Movement of organisms from one ecosystem to another with age as their resource requirements change'.	–	**Movement**, **dispersal**, **migration**, **isolation**, transfer, relay, spread, spillover, network, patches, subsidy, links, **linkages**,

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Table 1. *(Cont.)*

Concept	Exact term defined	Source	Realm(s) (continental, marine or both)	Focus of the paper	Proposed definition	Subcategories mentioned for the term (if any)	Connectivity key words used at least twice in the paper (words mentioned more than five times are in bold)
							connections, barriers, **boundaries**.
	(Population) Ecological connectivity	Cramer *et al.* (2023)	Mainly marine (theoretical)	Theory in conservation science	'The mixing of individuals in space and time'. or 'The movement of organisms across a landscape'.	Demographic Connectivity, Migratory Connectivity	**Movement**, **dispersal**, **migration**, **gene flow**, isolation, patch(es), corridor, **connections**, **interactions**, **metapopulation**, **population structure**, **subpopulations**, range.
Trophic connectivity	Trophic connectivity	Bishop *et al.* (2017)	Marine	Marine environmental science	'The strength and nature of trophic interactions that transfer energy and nutrients across habitat boundaries'.	–	**Movement**, **dispersal**, **migration**, **transport**, **flow**, **spread**, spillover, shift, expansion, **patches**, **subsidies**, **corridors**, pathways, patterns, interactions, **barriers**, **boundaries**, fragmentation, **stepping stones**, **source**, sink, metapopulation, range.
	Trophic connectivity	Olds *et al.* (2018)	Marine	Theory in seascape ecology	'Spatial effects of one ecosystem on food web structure in another'.	–	**Movement**, **dispersal**, **migration**, **isolation**, transfer, relay, spread, spillover, network, patches, subsidy, links, **linkages**, **connections**, barriers, **boundaries**.

MPA, Marine Protected Area.

habitat patches or communities (e.g. Carr *et al.*, 2017; Beger *et al.*, 2022).

Although most recent studies in marine science advocate for a division between 'structural' and 'functional' connectivity (e.g. Carr *et al.*, 2017; Balbar & Metaxas, 2019; Hilty *et al.*, 2020; Beger *et al.*, 2022), the nature of MFC and its boundaries remains obscure across the literature. Even when functional connectivity at sea is used to refer only to the movement of organisms (see Table 1), it is facilitated (or hampered) by either 'structural' connectivity alone (e.g. Balbar & Metaxas, 2019; Hilty *et al.*, 2020), or by a combination of the effects of the 'structural' connectivity of the land/seascape (i.e. its geomorphological heterogeneity) and a complementary type of connectivity corresponding to the advection and diffusion of water, referred to as '(passive) oceanographic' or 'hydrological' connectivity (e.g. Saunders *et al.*, 2016; Keeley *et al.*, 2021). Further debate considers whether structural and functional connectivity together constitute the 'actual' or 'realized' ecological connectivity between marine systems, or if 'realized' ecological connectivity is simply an attribute of MFC, once the various aspects of species biology and ethology (e.g. swimming behaviour, survival) have been considered (Table 1). This lack of consistency confuses attempts to identify knowledge gaps or to apply management measures, especially as ecological connectivity terminology and subcategories vary by scientific discipline and research intent (Table 1, Fig. 2; see Appendix S2).

For instance, the 4093 articles that specifically address 'connectivity' within the published literature on marine species movement and distribution fall into three distinct semantic groups (see the colour-defined clusters in Fig. 2), each describing spatial flows or interconnections differently. Notably, while most articles use the term 'dispersal', it is most common in studies that applied connectivity modelling, particularly for early life stages (green cluster). To date, authors in this area (green cluster) mostly paired 'dispersal' with the terms 'self-recruitment' and 'transport', while papers from the field of genetics (red cluster) favoured terms such as 'gene flow' and 'population/genetic structure' and articles that applied natural or artificial tagging methods (blue cluster) more frequently employed terms like 'migration', 'movements' and 'colonization'. Interestingly, this interdisciplinary difference in terminology – particularly pronounced for papers dealing with genetics – is also observed in the small subset of these articles that specifically focused on 'functional

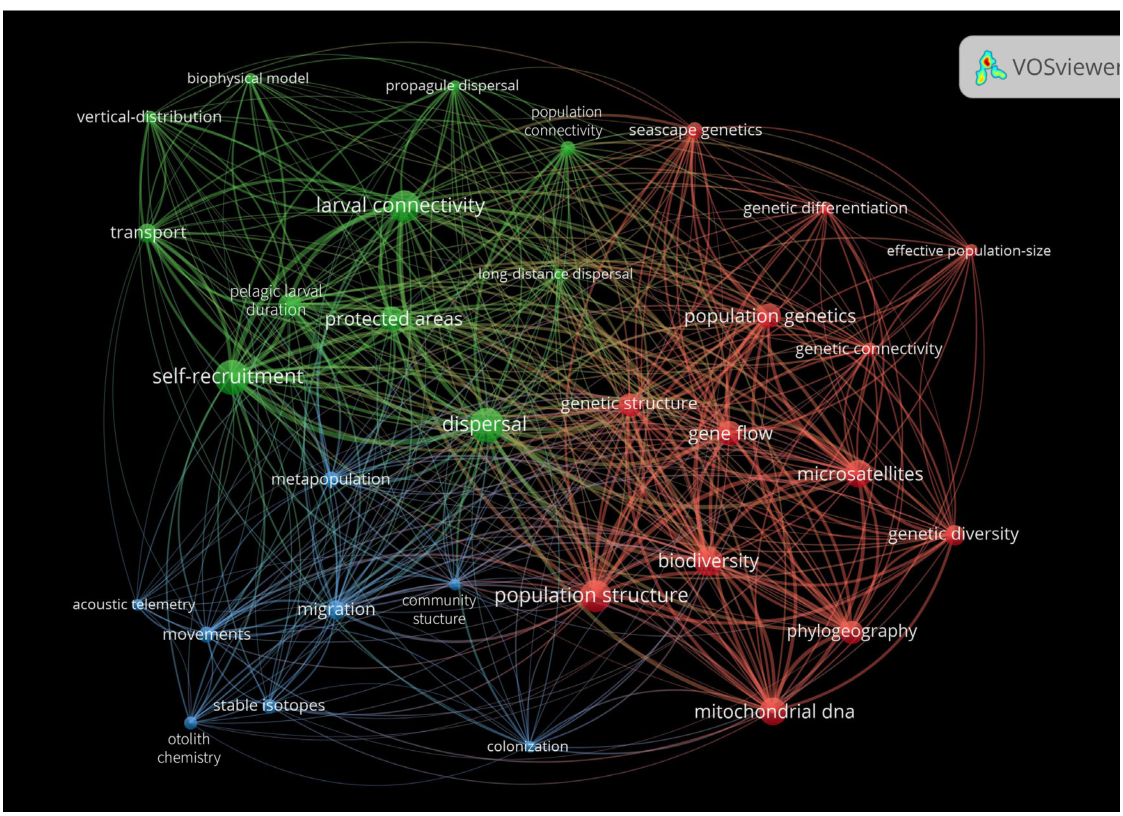

Fig. 2. Co-occurrence network map (VOSViewer co-occurrence network analysis; Van Eck & Waltman, 2010) for the main methodological and connectivity terms shared (co-occurrence ≥50) by the 4093 scientific articles from the literature search for Fig. 1 that specifically included the term 'connectivity'. On the graph, colours (red, green and blue) represent the three distinct terminology clusters identified by the analysis. Node size for each term illustrates its total number of co-occurrences (50–829), reflecting its relative importance within the network. The boldness of the link between two term nodes indicates the strength of their co-occurrence. For more information regarding the production of this figure, see Appendix S2.

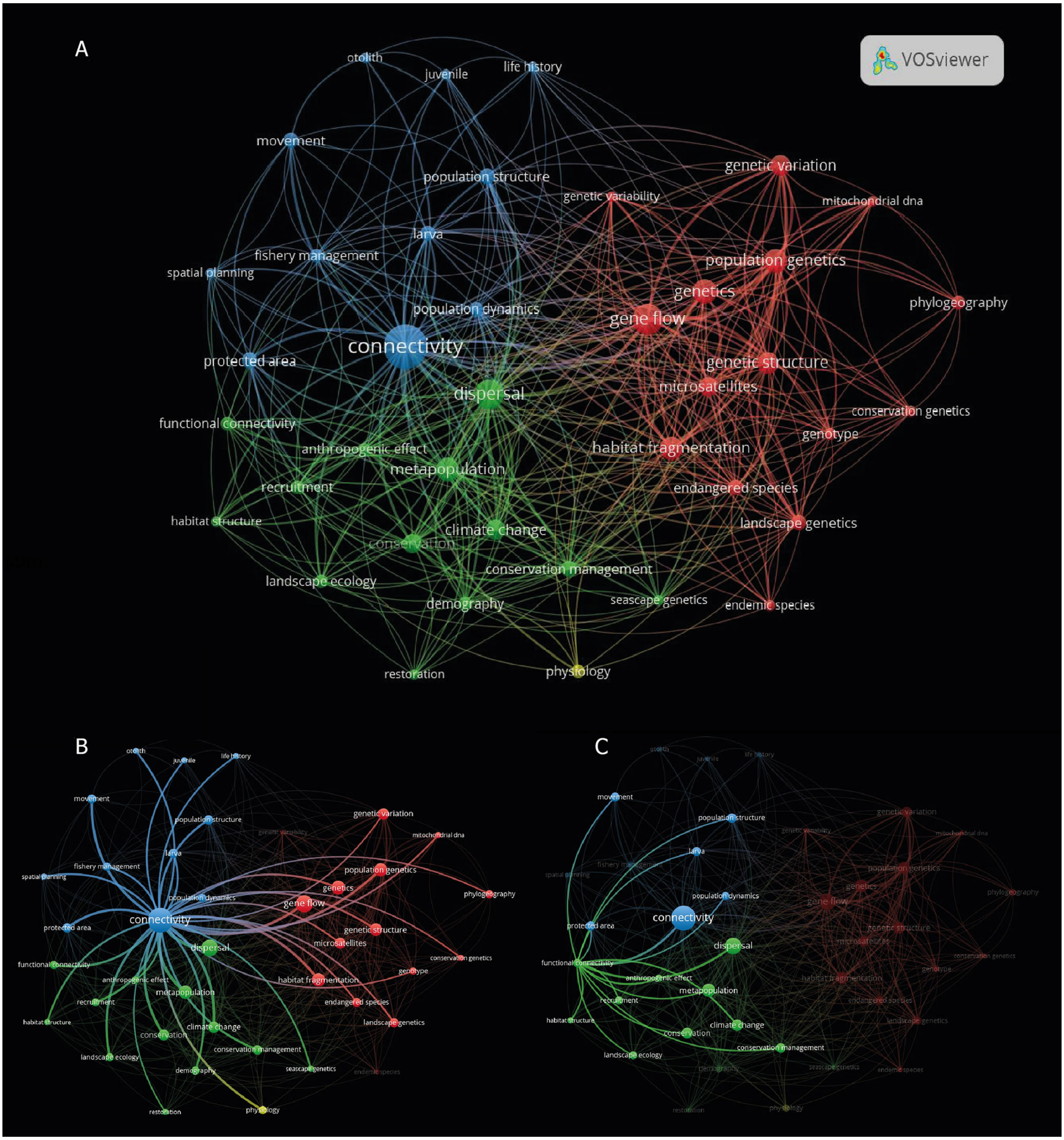

Fig. 3. Variation in terminology in the literature that has specifically addressed marine functional connectivity (MFC) to date. (A) Global co-occurrence network map (VOSViewer co-occurrence network analysis; Van Eck & Waltman, 2010) for the main methodological and connectivity terms shared (co-occurrence ≥5) by the 90 scientific articles from the literature search for Fig. 1 that specifically included the term 'functional connectivity'. (B, C) Specific co-occurrence networks for the terms 'connectivity' (B) and 'functional connectivity' (C) among the same articles. In all three graphs, colours (red, green, blue, and yellow) represent the four distinct terminology clusters identified by the co-occurrence network analysis. Node size for each term illustrates its total number of co-occurrences, reflecting its relative importance within the network. The boldness of the link between two term nodes indicates the strength of their co-occurrence. For more information regarding the production of this figure, see Appendix S3.

connectivity' (Fig. 3, see Appendix S3), which form four distinct semantic groups (see the colour-defined clusters in Fig. 3A). All make extensive use of the term 'connectivity' (Fig. 3B), but while references to 'functional connectivity' are common in articles on resource management and on conservation/spatial planning (green and blue clusters), they have yet to become widely adopted by both the genetics (red cluster) and physiology (yellow cluster) research fields (Fig. 3C). Furthermore, when MFC is subcategorized, for example by distinguishing between 'active' *versus* 'passive' connectivity, or between 'genetic', 'ontogenetic' and 'trophic' connectivity, the definitions and boundaries of subcategories vary among disciplines and research goals (Table 1), together with the specific terminology used to describe spatial exchanges (e.g. 'movement', 'dispersal', 'transfer', 'flow', 'shift', 'exchanges', 'spread' or 'spillover') and interconnections (e.g. 'networks', 'mixing', 'connections', 'linkages' or 'corridors').

This variability augments the lack of common understanding of the concepts and processes involved in MFC. However, confusion around the definition of 'functional connectivity' also stems from the ambiguity still inherent in the word 'function' in ecology, which alternatively denotes ecological processes, the roles or services of species or habitats, and/or the functioning of entire systems (Jax, 2005; Morrow, 2023). This confusion has been fuelled by recent developments in 'functional ecology' aiming to link movement and trait expression in marine species to ecosystem structure and functioning (Brandl *et al.*, 2019; Anderson & Fahimipour, 2021; Fontoura *et al.*, 2022). As a result, while most current definitions of MFC focus purely on the movement of living organisms, some marine scientists also include the effects of these movements on ecosystem processes (e.g. nutrient cycling, wave attenuation) and/or the abiotic transport of non-living matter (e.g. inorganic nutrients, detritus), which are also integral for ecosystem functioning (Table 1). We argue against these additions, which only increase conceptual confusion by leading towards redundancy with the current definitions of 'ecological connectivity'. Even if the main approaches and tools describing the abiotic transport of inorganic matter (in oceanography, hydrology, sedimentology, or geomorphology) help to infer the dispersal patterns of marine organisms, accurate prediction of the distribution and movements of marine life requires vital complementary information on the behaviour, biology, and physiology of species. As environmental patchiness incorporates the distribution of inorganic matter and detritus, we advocate that the abiotic transfer of non-living matter (e.g. by currents or gravity) is considered a driver rather than an intrinsic component of MFC.

Similarly, because studying the multiple effects of biodiversity on the functioning of ecosystems is particularly complex and has given rise to an entire field of research, BEF (Thompson *et al.*, 2012; Gonzalez *et al.*, 2020), we believe it is more practical to consider MFC as a separate ecological process, which only defines the qualitative and quantitative compositions of ecosystems (including biodiversity), regardless of the impact these may or may not subsequently have on ecosystem functioning through BEF interactions.

Building on past definitions, the current diversity of approaches, and uses of ecological connectivity, we propose the following, hopefully more practical, overarching definition, contours, and structuring for MFC science. We advocate for MFC to specifically refer to *the functional links between distinct areas, ecosystems or habitat patches, at sea and at the land–sea interface, that result from all the flows (of individuals, gametes, propagules, matter, compounds and energy) caused by the combined lifetime and transgenerational displacements of marine organisms* (Table 2). As such, MFC encompasses both the progressive dispersal of marine species (from bacteria to top predators) across generations and the lifetime trophic and ontogenetic movements (as eggs, larvae, propagules, juveniles, subadults and/or adults) of the many living organisms that use the marine space (Fig. 4). These varied displacements all result in spatial flows of biomass, genotypes, phenotypes (functional traits), energy and information, but also in indirect transfers of organic matter and nutrients *via* waste excretion. Through this definition, MFC can be seen as a dynamic global ecological process, distinct but integral to overall ecological connectivity (Fig. 4), with its own unique contours, evaluation methods and evolutionary patterns. It also becomes truly 'functional', as the dynamic spatial interactions between marine (sub)populations, species assemblages or communities drive most of the functional links (within and between ecological systems) that sustain ecological processes and services. Defined in this way, MFC governs the flows of biomass, genotypes, and phenotypes (functional traits) across marine habitats, depths, ecosystems, areas and regions, but also a vast part of the flows of organic matter, compounds, nutrients, energy and disturbance between them (Table 2, Fig. 4). This also applies at the land–sea interface, *via* the complex life cycles of many species that migrate across realms.

In parallel, we argue that, while encompassing both a geomorphological component ('land/seascape structural connectivity') and a hydrological component ('hydrological structural connectivity') (Table 2), structural connectivity (SC) in aquatic environments should focus uniquely on the physical spatial relationships among land/seascape elements. This perspective underlines the specificity of spatial abiotic fluxes (e.g. the transfer of non-living matter by currents or gravity) and their role in ecosystem functioning. It also allows highlighting the importance of the spatial arrangement of land/seascape elements for ecological connectivity, including how the physical configurations of ecological networks either facilitate or constrain MFC, through factors such as physical or chemical barriers (e.g. water stratification), hydrological pathways (e.g. currents, internal waves, tidal bores), and migration corridors (Table 2). Crucially, although MFC can be caused, facilitated, or impeded by both hydrological and land/seascape structural connectivity, it is ultimately driven by the specific biology and ecology of marine species (e.g. morphology, physiological niche, life-history traits,

Table 2. Suggested refined subcategories in marine ecological connectivity Science and their proposed definitions.

Subcategories	Proposed definitions	Supporting references
Structural connectivity (SC)	**The physicochemical heterogeneity and structuring in the abiotic environment and the physical links between distinct areas, ecosystems, depths or habitat patches, at sea and at the land–sea interface**. *It can be inferred between discrete habitat patches, depths, ecosystems, areas or regions.*	Tischendorf & Fahrig (2000); Auffret *et al.* (2015); Hilty *et al.* (2020); Beger *et al.* (2022)
Land/Sea-Scape SC	**The degree to which physicochemical heterogeneity and structuring in the landscape/seascape facilitate or impede movement and flows among distinct areas, ecosystems, depths or habitat patches, at sea and at the land–sea interface**. *It can be inferred between discrete habitat patches, depths, ecosystems, areas or regions.*	Grober-Dunsmore *et al.* (2007); Caldwell & Gergel (2013); Olds *et al.* (2016); Beger *et al.* (2022)
Hydrological SC	**The degree to which the advection and diffusion of water facilitate or impede movement and flows among distinct areas, ecosystems, depths or habitat patches, at sea and at the land–sea interface**. *It can be inferred between discrete between discrete habitat patches, depths, ecosystems, areas or regions.*	Freeman *et al.* (2007); Saunders *et al.* (2016); Keeley *et al.* (2022)
Marine Functional Connectivity (MFC)	**The functional links between distinct areas, ecosystems or habitat patches, at sea and at the land–sea interface, that result from all the flows (of individuals, gametes, propagules, matter, compounds and energy) caused by the combined lifetime and transgenerational displacements of marine organisms**. *It can be inferred at the population, species, taxa, assemblage or community scale and is facilitated or hampered by both structural connectivity and marine organisms' biology and behaviour.*	Tischendorf & Fahrig (2000); Kindlmann & Burel (2008); Grober-Dunsmore *et al.* (2009); Olds *et al.* (2016); Darnaude *et al.* (2024)
Passive MFC	**The functional links between distinct areas, ecosystems or habitat patches that result from all the flows (of individuals, gametes, propagules, matter, compounds and energy) caused by the passive indirect transport of marine organisms (dead or alive), either by oceanographic processes or via the active movements of other species**. *It is facilitated or hampered by both structural connectivity and organisms' biology, morphology and behaviour*, in variable proportions depending on the mean of transport (oceanographic or vector-driven).	Hidalgo *et al.* (2017); Villarino *et al.* (2018); Cannizzo *et al.* (2021); Johansen *et al.* (2021)
Oceanographic MFC	**The functional links between distinct areas, ecosystems or habitat patches that result from all the flows (of individuals, gametes, propagules, matter, compounds and energy) caused by the passive transport of marine organisms (dead or alive) through physical or hydrological processes such as currents, sinking or upwelling**. *It is mainly driven by hydrological connectivity, although landscape/seascape structural connectivity and marine organisms' biology and behaviour also facilitate or hamper it.*	Hidalgo *et al.* (2017); Villarino *et al.* (2018); Cannizzo *et al.* (2021); Johansen *et al.* (2021)
Vector-Driven MFC	**The functional links between distinct areas, ecosystems or habitat patches that result from all the flows (of individuals, gametes, propagules, matter, compounds and energy) caused by the passive transport of some marine organisms (dead or alive) through the active movements of other species. It includes both the host-driven dispersal of parasites, symbionts, viruses or bacteria and the human-mediated indirect transport of marine species**. *It is mainly driven by the biology and behaviour of species, as it is mainly achieved through the active movements of vector species (including humans).*	Carlton & Ruiz (2015); Vlok, Lang & Suttle (2019); Dittami *et al.* (2021); Mony *et al.* (2022)
Active (migratory) MFC	**The functional links between distinct areas, ecosystems or habitat patches that result from all the flows (of individuals, matter, compounds and energy) caused by the purposeful, self-directed active movements of living marine organisms**. *It is mainly driven by species biology and behaviour, although local structural connectivity can facilitate or hamper it.*	McMahon *et al.* (2013); Cannizzo *et al.* (2021); Johansen *et al.* (2021)

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Table 2. *(Cont.)*

Subcategories	Proposed definitions	Supporting references
Evolutionary (Transgenerational) MFC	**The functional links between distinct areas, ecosystems or habitat patches that result from all the flows (of individuals, matter, compounds and energy) caused by the transgenerational shifts in distribution of marine populations, through the combined dispersal, survival and reproductive success of their individuals**. *It results in what people commonly refer to as 'genetic' or 'demographic' connectivity (*Table 1*), but not exclusively, and is driven by a variable mix of passive and active (migratory) FC, depending on species biology, behaviour and local structural connectivity*.	Leis *et al.* (2011); Cramer *et al.* (2023)
Lifetime (Experiential) MFC	**The functional links between distinct areas, ecosystems or habitat patches that result from the spatio-temporal exchanges (of individuals, gametes, propagules, matter and energy) caused by the combined displacements of marine organisms over their lifespan**. *It includes what people commonly call 'ontogenetic' connectivity (*Table 1*) and is mainly driven by species biology and behaviour, although hydrological and land/sea-scape connectivity also facilitate or hamper it.*	Clark *et al.* (2009); Quevedo, Svanbäck & Eklöv (2009); Bergamino *et al.* (2014); Beger *et al.* (2022)
Qualitative MFC	**The differential spatial flows (of genotypes, phenotypes, species traits, specific compounds or information) caused by the combined lifetime and transgenerational displacements of marine organisms that modulate the qualitative composition of populations, communities and ecosystems, impacting their structure, evolution and resilience through changes in genetic, taxonomic and functional biodiversity**. *It includes (but is not restricted to) what people commonly call 'genetic' connectivity (*Table 1*), and occurs at varied timescales, driven by a variable mix of passive and active (migratory) MFC, depending on species biology and behaviour and on local structural connectivity*.	–
Quantitative MFC	**The directional spatial fluxes (of matter, chemical elements or energy) caused by the combined lifetime and transgenerational displacements of marine organisms that shape the quantitative composition of ecosystems, impacting their productivity and functioning through changes in material cycling and flows within food webs**. *It includes (but is not restricted to) what people commonly call 'trophic' connectivity (*Table 1*), and occurs at varied time scales, driven by a variable mix of passive and active (migratory) MFC depending on species biology and behaviour and on local structural connectivity*.	–

ethology, behaviour) interacting with local environmental settings, including nutrient concentrations and abiotic material fluxes that are themselves partly shaped by structural connectivity.

Thus, although 'potential' MFC can arise from both structural connectivity and species biology, the 'realized' MFC represents the manifestation of the two components combined. This distinction is important, as it allows us to quantify the role that marine species (and biodiversity more broadly) play in governing the functioning of the global ocean and of our planet through realized ecological connectivity, within ecosystems ('ecosystem connectivity') and across them ('ecoscape connectivity' or 'land/seascape connectivity') (Table 1). This conceptual scheme for marine ecological connectivity science, along with the delineation of the boundaries of MFC research that it provides, will ensure that future research is gathered under a coherent and practical framework, facilitating broad uptake across research fields and end users, and improved transferability to guide sustainable blue growth and marine conservation.

However, reduction in the redundancies, overlaps and terminological confusion among existing MFC subcategories is also required, while highlighting the complex, dynamic interplay between its various facets. In this context, we propose unifying previous terminology and definitions (Table 1) into the following eight MFC subcategories, based on what is exchanged at sea and at the land–sea interface, and how (Fig. 4, Table 2). To reflect the main modes of movement of marine organisms, we propose a first distinction between 'active (migratory)' *versus* 'passive' MFC (Table 2), the latter resulting either from the passive drift of marine species in the water column through oceanic processes like currents or

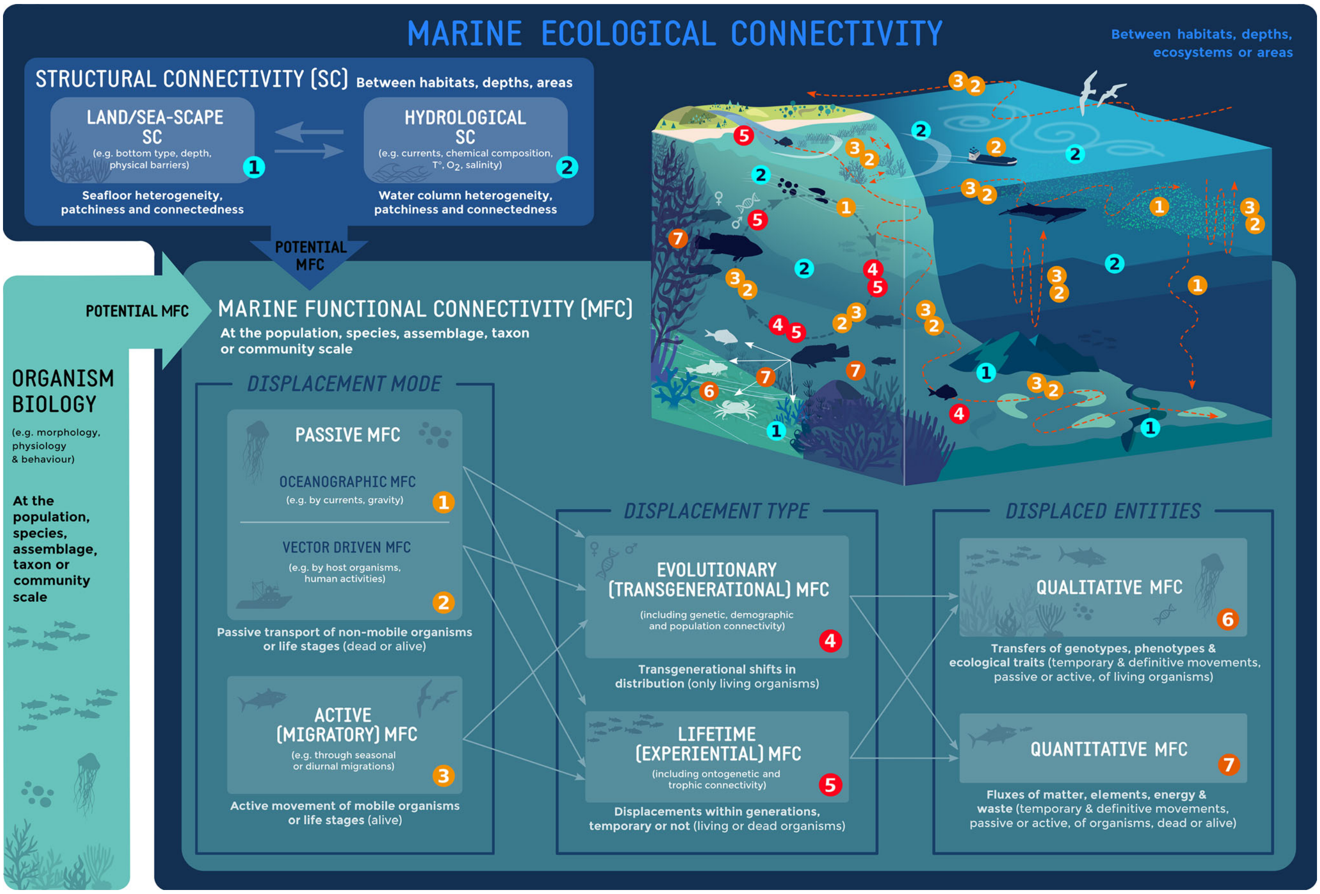

Fig. 4. Proposed boundaries and subcategories for Marine Functional Connectivity (MFC) within the multifaceted concept of marine ecological connectivity. T°, temperature.

gravity ('oceanographic MFC') or, for some taxa, from the active directed movements of other species, including humans ('vector-driven MFC'). This first distinction is justified by the methodological differences used to describe these three displacement modes, all of which have different drivers (Table 2). Indeed, although partly influenced by organisms' behavioural responses (e.g. larval reactions to environmental cues), oceanographic MFC is primarily driven by currents and water column stratification. Therefore, it is mainly described using biophysical modelling, while active (migratory) MFC, resulting from animal migration, is usually assessed using telemetry or natural tags (Sturrock *et al.*, in press). Because vector-driven MFC is a complex outcome of the biology and ethology of both the transported and transporting species, its description requires the integration of approaches from a diverse set of disciplines, especially when trying to infer human-mediated dispersal (Mony *et al.*, 2022; Agiadi *et al.*, 2024). The second distinction we propose is intended to contrast the two main types of displacement of living organisms along the time continuum, either progressive and occurring across generations ('evolutionary (transgenerational) MFC'; Table 2) or transient and restricted to within the lifetime of the individual ('lifetime (experiential) MFC'). Again, the approaches, technologies and tools applied to describe these movements, and the spatial and temporal scales at which they occur, differ substantially (Cramer *et al.*, 2023). While evolutionary (transgenerational) MFC is usually inferred over extended timescales (decades to millennia) using genetics, lifetime (experiential) MFC estimation usually combines the use of natural or applied tags with distribution or biophysical modelling to infer movements on timescales usually ranging from days to decades (Sturrock *et al.*, in press). The final distinction relates to the intrinsic traits and composition of organisms, as well as the nature of the diverse properties and entities they transfer through movement, in relation to the two functional dimensions of biodiversity: qualitative and quantitative (Fig. 4, Table 2). For instance, individuals from rare species, locally adapted populations, or species migrating across contrasting habitats or realms may be unique in their qualitative composition (e.g. through distinctive fatty acid profiles, rare alleles, or uncommon functional traits), yet redundant with many others in terms of biomass or carbon content. Conversely, some organisms, such as whales, contribute unparalleled quantities of biomass and chemical elements when they move, generating distinctive quantitative fluxes of matter and energy. We therefore propose to distinguish between 'qualitative MFC' (the differential transfer *via* organism movements of specific genotypes, phenotypes, compounds, and functional traits, which alter the qualitative composition of interconnected populations, communities and ecosystems) and 'quantitative MFC' (the directional transfer of individuals, matter, energy and chemical elements that change their quantitative content) (Fig. 4, Table 2). Although these two facets of MFC are complementary and often intertwined, distinguishing between them makes MFC more explicitly 'functional' and more readily applicable across research fields, by addressing both what is exchanged between areas and how the exchange affects the composition, structure, and functioning of populations, communities, and ecosystems. This distinction should also facilitate the integration of MFC data into most complementary research disciplines in marine environmental science (Fig. 5), which focus either on species or ecosystem health and resilience (mainly linked to qualitative MFC) or on ecosystem productivity and functioning (mainly linked to quantitative MFC). Importantly, these two MFC subcategories require different observation tools and modelling approaches, as the fluxes they involve differ substantially (Table 2). Quantifying them both demands unprecedented interdisciplinary integration of data, but is essential for sustaining a healthy, resilient, productive, and functioning ocean.

(2) A new conceptual framework placing MFC at the core of marine ecology research

The multidisciplinary field of MFC research, as defined above, promises to stand at the very core of marine environmental science by providing the conceptual and methodological foundation for establishing a uniquely integrative link among disciplines assessing the responses of the ocean and its species to global change and disciplines involved in modelling ecosystem dynamics and services (Fig. 5).

The refined subcategories of marine ecological connectivity (Table 2) capture the multifaceted nature of MFC and help coordinate the diverse research approaches applied in this field. This will facilitate the investigation of spatial, temporal and taxonomic variability in MFC, and its drivers and consequences. Building on the complementary information gathered through genetics, natural tags and telemetry – but also through the modelling of species dispersal and distribution – will enable us to describe the past, present and future spatial fluxes of individuals, genes, biomass, and energy that largely drive the quantitative and qualitative compositions of marine ecosystems. Investigating the mid- and long-term dynamics of MFC, largely ignored until now, will also allow a significantly advanced understanding of the diversity, stability, functioning and

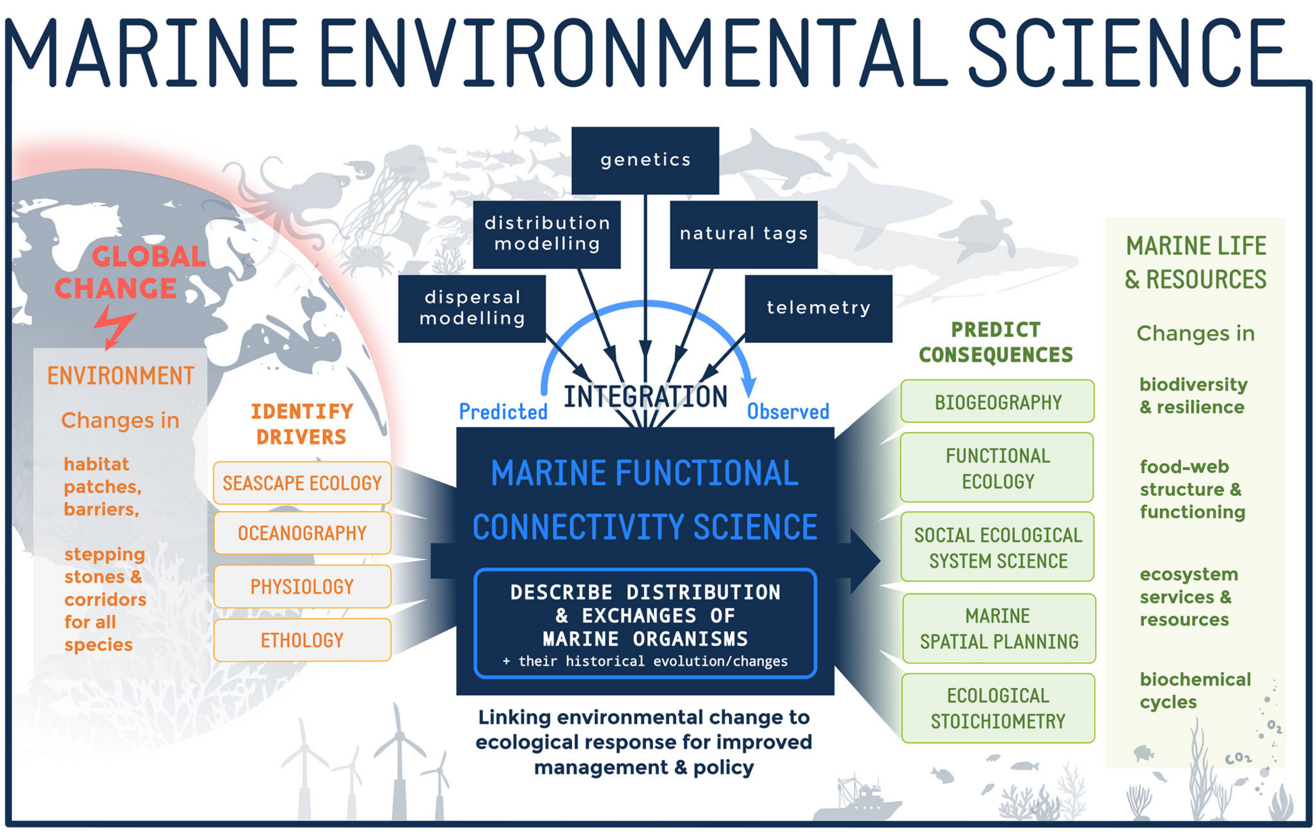

Fig. 5. Conceptual framework for the structuring and positioning of the emerging field of marine functional connectivity (MFC) research within marine environmental science.

potential resilience of marine socio-ecological systems (Darnaude *et al.*, 2022, 2024).

A holistic perspective on MFC is the missing component for a truly multidimensional understanding of ecological processes in marine systems, clarifying the mechanisms involved from pressure effects (e.g. changes in habitat patches and species dispersal pathways) to ecological responses (e.g. changes in biodiversity, ecosystem productivity and resilience, or in biogeochemical cycles) (Fig. 5). Because the unified research field of MFC science will necessarily interact with complementary disciplines that study MFC drivers and constraints (e.g. seascape ecology, oceanography, physiology, and ethology), and MFC consequences (e.g. biogeography, functional ecology, socio-ecological system science and ecological stoichiometry), MFC science will be pivotal for bridging research on the current status and vulnerability of marine habitats and species with predictions of the future of the ocean and its services (Fig. 5). Ultimately, this will be transformative for forecasting how environmental and anthropogenic factors may alter marine ecosystem services and productivity, and for developing adequate strategies to mitigate these effects.

The framework proposed here lays the foundation for deeper insights into the complex interdependencies between environmental conditions and biological communities across habitats, depths, ecosystems and regions. It also facilitates cross-realm investigations of ecological connectivity and its consequences, since the restructured terminology proposed here can readily be extended beyond the marine realm and adapted to continental environments (aquatic or terrestrial). Such integration is essential for addressing pervasive gaps in our understanding of marine biodiversity and ecosystem change, and for establishing the scientific framework needed to guide sustainable development in the face of global change (Muller-Karger *et al.*, 2024).

IV. FUTURE AVENUES FOR MFC SCIENCE

Achieving the necessary level of monitoring, understanding and application of MFC in the near term requires rapid, multi- and transdisciplinary progress. Recent advances in methodology and tools are already driving research and management in this direction. Building on these, we highlight the most promising avenues for future developments in relation to the three main challenges outlined in Section II.

(1) Moving towards fully integrated MFC research

Protecting the oceans and their services under increasing human pressures and climate change requires MFC patterns to be mapped, and their drivers and consequences unravelled. Success here necessitates an interdisciplinary approach, encompassing biodiversity and socio-ecological systems. Growing links between previously unconnected disciplines point towards movement in this direction. For instance, integrating genetics, modelling, and geohistorical time series of species abundances offers unique insights into shifts in MFC patterns over time and the response of marine ecosystems to increasing human pressures (Agiadi *et al.*, 2024). Likewise, combining natural tags with telemetry can yield otherwise unavailable insights into the spatial and temporal movements of migratory species and their lifetime functional roles, which are crucial for guiding sustainable marine resource management (Darnaude & Hunter, 2018; Daban *et al.*, 2024; Hüssy *et al.*, 2024). Transdisciplinary knowledge integration is also essential to understand the basics of many cryptic aspects of MFC, for which data are severely lacking. This includes the many spatial flows between discrete habitats that result from the transport of parasites, diseases or symbionts by their hosts, or from human-mediated dispersal (e.g. translocation *via* shipping activities, hatcheries or aquaculture escapees, species introductions). The significance of these flows is only just beginning to be assessed (e.g. Sinclair *et al.*, 2020; Einfeldt, Jesson & Addison, 2020; Hendrick *et al.*, 2024), as their quantification demands the integration of data from diverse natural and social science disciplines (Carlton & Ruiz, 2015; Mony *et al.*, 2022; Agiadi *et al.*, 2024). However, addressing this knowledge gap is an urgent priority, particularly regarding the human-mediated dispersal of marine species, as our activities represent the ultimate long-distance transport vector for numerous marine organisms. Clarifying the role of plasticity in life-history strategies and partial migration in MFC fluctuations is also in its infancy (e.g. Toledo *et al.*, 2020; Saboret *et al.*, 2021) but is key to the accurate prediction of meta-ecosystem dynamics and the capacity of marine species to adapt to changing environmental conditions (Peller, Guichard & Altermatt, 2023). Lastly, understanding MFC dynamics for rare species or those with unusual biological or functional traits, which often fulfil vulnerable yet significant inter-habitat ecological functions (Mouillot *et al.*, 2013), will be necessary to conserve marine socio-ecological systems effectively. Transdisciplinary approaches at the frontier between MFC science and functional ecology, which examines the roles of organisms and their interactions within ecosystems, pave the way for this (Chase *et al.*, 2020).

Building on this innovative transdisciplinary work will advance previous efforts to integrate approaches to MFC (see Sturrock *et al.*, in press), underpinning the compilation of comprehensive and multifaceted MFC data sets across all spatial, temporal, and organizational scales. The framework proposed here will allow re-evaluating existing MFC approaches and tools to help identify appropriate contexts for their combination and guide their integration from sampling and study design through to the production of integrated connectivity indices. Adoption of standardized global methodologies and publication of data in accessible and standardized formats, such as open data repositories, will further ensure data sharing across disciplines. Data platforms specifically designed for mapping marine biodiversity distribution and movement, such as those of the

Ocean Biodiversity Information System (OBIS) or the Migratory Connectivity in the Ocean website (https://mico.eco), can play a crucial role here. Ultimately, the successful implementation of MFC hinges on cultivating a new generation of genuinely interdisciplinary marine scientists. Encouraging cross-disciplinary training and education amongst early-career researchers can overcome disciplinary boundaries, improve knowledge and data sharing, and foster a more comprehensive understanding of MFC. Without this shift, we risk poor decision-making and maladaptation in the face of future marine change.

(2) Improving our understanding of MFC drivers and consequences

Advancing our understanding of changes in ocean biodiversity and functioning in the face of global change requires improved estimates and indices of MFC, and their integration into models that predict patterns and trends in spatial networks. From individual species to metacommunities and ecosystems, all organizational levels must be addressed. Again, this requires transdisciplinary integration. Linking MFC with species biogeography, physiology, ethology and/or with ecosystem resilience and functioning holds great promise, especially through approaches like conservation physiology (e.g. Cooke *et al.*, 2022), conservation behaviour (Cooke *et al.*, 2023), BEF science (e.g. Correia & Lopes, 2023) or ecological stoichiometry (e.g. Welti *et al.*, 2017). Indeed, knowledge of species' traits, including physiological niches, swimming abilities, life strategies, and sensory systems, helps to explain the capacity of species to disperse, survive, and connect habitats. Therefore, insights from physiology and ethology provide a valuable knowledge base of species' movement mechanisms and their ecological consequences. Integrating MFC and biogeographical research can further reveal how connectivity influences species distribution and community composition and structure (e.g. Azovsky *et al.*, 2020). Lastly, the study of species interactions, such as predation, symbiosis and parasitism, can help pinpoint synergies in species distribution and dispersal (Coll *et al.*, 2020). Emerging predictive models for complex species movement are already advancing this work (e.g. Malishev & Kramer-Schadt, 2021; Friesen *et al.*, 2021). Building on such models, future research should explore how species traits mediate connectivity at the multi-species level.

Multi-species connectivity modelling approaches are emerging in terrestrial ecology [see Wood *et al.* (2022) for a review] but have yet to be adapted to marine contexts. Nevertheless, promising conceptual models have been developed at the intersection between BEF and Food Web Theory (FWT) to predict biodiversity's impact on ecosystem functioning and services (Hines *et al.*, 2015; Wood *et al.*, 2022). These models pave the way to incorporate multiple species interactions into MFC assessment, thereby offering a more accurate representation of how interspecific interactions influence habitat use, movement, and the long-term persistence of metacommunities (Thompson *et al.*, 2018; Chase *et al.*, 2020). Applying these models will enable a shift in connectivity conservation from merely 'stacking' habitat networks or metapopulations to developing multiplex ecological networks across ecoscapes (Strydom *et al.*, 2021). Furthermore, incorporating MFC into trait-based BEF approaches will enhance our understanding of how connectivity influences key ecological processes such as nutrient cycling and energy flow. This will highlight the role of MFC in maintaining ecosystem stability, productivity, and resilience (Coux *et al.*, 2016; Schleuning, García & Tobias, 2023). Specifically, synthesis of these data can identify 'keystone MFC species', integral to the functionality of the global marine network. The mapping of current and future hotspots of MFC across regions, depths, and realms, at sea and at the land–sea interface, is also a fundamental tool to boost management for sustainable ecosystems and resources. As the movement of organisms affects nutrient transport and cycling, linking MFC to ecological stoichiometry will further aid mapping of global element distribution and flows (Welti *et al.*, 2017). Finally, building on recent modelling advances that integrate MFC research with socio-ecological system science on land (e.g. Pashanejad *et al.*, 2024) will allow exploration of how connectivity affects and is affected by human activities and marine resource sustainability. This will support better-informed decision-making and the development of effective conservation strategies that account for marine ecological connectivity. To understand fully the impact of MFC on ocean functioning, interdisciplinary research should focus on: (1) exploring the significance of both horizontal and vertical connectivity across different ocean provinces and scales; (2) identifying the optimal levels of connectivity between marine ecosystems and communities to sustain ecosystem services, including resilience and productivity; and (3) evaluating whether maintaining MFC at these levels can enhance the resilience of marine ecosystems to future environmental pressures.

(3) Removing barriers to provide relevant MFC data and decision-making tools

With the growing recognition that spatial interactions across habitat patches must be considered in environmental or resource-management plans (Hillman *et al.*, 2018), frameworks enabling reproducible, pragmatic connectivity measures are being actively pursued. Solutions are also emerging that will overcome barriers to incorporating MFC knowledge into environmental policy and management at all levels. A variety of applied connectivity metrics are already available, derived from genetics, network analysis, parentage analysis, biophysical models, and biomass or morphometric gradients (Buchholz-Sørensen & Vella, 2016; Williamson *et al.*, 2016; Keeley *et al.*, 2021). Metrics such as local retention, betweenness centrality, and outflow are particularly useful for Marine Protected Area (MPA) design (Magris *et al.*, 2018; Muenzel *et al.*, 2023). However, there remains a need for the development of new spatial planning and decision-making support tools integrating and prioritizing connectivity criteria and metrics (Depellegrin *et al.*, 2021). Improved software, such as Marxan and Zonation, combined with new tools like 'Marxan Connect' (Daigle *et al.*, 2020; https://marxanconnect.ca/), and other free tools that integrate novel connectivity-related algorithms (e.g. BlueBioSites https://gis.sea.ee/bluebiosites/), can help guide effective spatial prioritization in conservation planning. Building on these tools will support informed decision-making by stakeholders at multiple spatial, temporal, and organizational scales (Balbar & Metaxas, 2019; Daigle *et al.*, 2020; Andrello *et al.*, 2022; Beger *et al.*, 2022).

While metrics quantifying seascape patterns across multiple scales can be more easily communicated than full simulation models (Cumming *et al.*, 2022), the complexity and uncertainties of many MFC patterns and their impact on ocean ecosystems make it difficult to convey MFC metrics fully to decision-makers (Beger *et al.*, 2022). Web-based decision support tools that run full models using preferred scenario simulations and data-driven management actions can help translate connectivity issues without oversimplifying the analyses. However, the tailoring of such tools to the needs of decision-makers and practitioners is necessary to integrate complex connectivity considerations effectively into biodiversity management. Notably, the incorporation of MFC data in the now-established Ecosystem-Based Management (EBM) approach is still in its infancy, as it requires the development of appropriate models to predict patterns and changes in MFC at community and ecosystem scales (Schill *et al.*, 2015; Williamson *et al.*, 2016). Recent methodological developments incorporating connectivity into models to guide Ecosystem-Based Marine Spatial Planning (EBMSP) and Ecosystem-Based Fisheries Management (EBFM) provide a good example of the way forward (Petza *et al.*, 2023). Multilayer spatial networks modelling is also particularly promising, as it enables integration of complex data on abiotic environmental drivers, interactions between individuals or species, but also co-dependency of human activities and ecosystem services (Madeira *et al.*, 2024; Pashanejad *et al.*, 2024). Although new to spatial management, this approach offers valuable guidance for marine interventions by identifying key components for the functioning of socio-ecological systems and uncovering their interactions and conflicts. A next step will be the definition and development of connectivity guilds, based on species movement and life-history traits, and their integration into the models applied. Advancing these new avenues will undoubtedly enhance effective incorporation of complex connectivity considerations into the decision-support tools that run full models for EBMSP and EBFM. This will allow governance and place-based management challenges to be addressed across a wide range of scales, from local coastal communities to full marine ecosystems (Painting *et al.*, 2020; Cannizzo *et al.*, 2021).

Ultimately, adopting effective, adaptive management strategies based on MFC will require integrated ocean and land–sea regulation, incorporating standardized, harmonized frameworks for management and policy across varying spatial scales and timeframes (Cannizzo *et al.*, 2021; Muller-Karger *et al.*, 2024). Close collaboration with local management institutions and global governance bodies and increased transboundary collaboration will be necessary. Ensuring that existing MFC databases, knowledge, and tools are coherent, accessible, and used in real time by decision-makers, managers, and planners will also be key (Painting *et al.*, 2020; Beger *et al.*, 2022). Guidance to incorporate connectivity conservation issues into marine spatial planning is emerging, as illustrated by the Marine Connectivity Conservation 'Rules of Thumb' for MPA and MPA Network Design (Beger *et al.*, 2022). The projected impacts of climate change on connectivity must also be considered to generate innovative climate-smart management strategies, flexible both in time and space, to safeguard regional biodiversity. Four main categories of planning-based solutions are recognized in the IUCN *Guidelines for conserving connectivity through ecological networks and corridors* aimed at maintaining and enhancing connectivity: ecological corridors, protected areas, OECMs, and ecological networks (Hilty *et al.*, 2020). The challenge now is to bring these MFC components into everyday use.

V. CONCLUSIONS

(1) Marine environmental science is at a turning point. As with the concept of functional ecology in the early 2000s, the emerging concept of marine functional connectivity can take science, management, and policy a step further, by significantly improving our understanding of the functioning of our seas and oceans, and our ability to predict the responses of marine life to environmental change and the consequences for services to the people and the biosphere.

(2) Integrating the various disciplines that study the distribution and movement of marine species and their impacts into the unified and operational interdisciplinary marine environmental science framework proposed here holds the promise to achieve a more precise, comprehensive, and applied understanding of spatial interconnections at sea and at the land–sea interface, paving the way towards truly integrated environmental management at the global scale.

(3) The subcategories of marine connectivity introduced here not only streamline data integration with complementary research fields, facilitating linkage between hitherto poorly connected marine environmental science disciplines, but could also be readily extended beyond the marine realm, thereby fostering cross-realm integration in ecological connectivity assessments.

(4) The new conceptual and methodological framework proposed here places MFC research at the heart of

interdisciplinary collaboration for improved marine governance, sustainable resource management, and biodiversity conservation in the face of climate change and human impact.

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VII. DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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IX. SUPPORTING INFORMATION

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

Appendix S1. Methods and key results for Fig. 1.
Appendix S2. Methods and key results for Fig. 2.
Appendix S3. Methods and key results for Fig. 3.