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Discussion

Multilayer biological networks to upscale marine research to global change-smart management and sustainable resource use

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ABSTRACT

Human activities are having a massive negative impact on biodiversity and ecological processes worldwide. The rate and magnitude of ecological transformations induced by climate change, habitat destruction, over-exploitation and pollution are now so substantial that a sixth mass extinction event is currently underway. The biodiversity crisis of the Anthropocene urges scientists to put forward a transformative vision to promote the conservation of biodiversity, and thus indirectly the preservation of ecosystem functions. Here, we identify pressing issues in global change biology research and propose an integrative framework based on multilayer biological networks as a tool to support conservation actions and marine risk assessments in multi-stressor scenarios. Multilayer networks can integrate different levels of environmental and biotic complexity, enabling us to combine information on molecular, physiological and behaviour responses, species interactions and biotic communities. The ultimate aim of this framework is to link human-induced environmental changes to species physiology, fitness, biogeography and ecosystem impacts across vast seascapes and time frames, to help guide solutions to address biodiversity loss and ecological tipping points. Further, we also define our current ability to adopt a widespread use of multilayer networks within ecology, evolution and conservation by providing examples of case-studies. We also assess which approaches are ready to be transferred and which ones require further development before use. We conclude that multilayer biological networks will be crucial to inform (using reliable multi-levels integrative indicators) stakeholders and support their decision-making concerning the sustainable use of resources and marine conservation.

1. Introduction

The increasing human footprint on Earth, related with the intensity and nature of our activities and our ever-increasing demography, has led to the substantial modification of geological, climatological and ecological processes and features (Caldeira and Wickett, 2003;

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Habersack et al., 2014; Payne et al., 2016; Sokolov et al., 2009; Waters et al., 2016). Human activities are therefore shaping species' developmental and eco-evolutionary trajectories (Palumbi, 2001; Pelletier and Coltman, 2018; Vitousek et al., 1997). Climate change, habitat fragmentation, resource exploitation, pollution, and invasive species are considered the most important and widespread anthropogenically-driven causes of change in biodiversity (Bowler et al., 2020; IPBES, 2019; IPCC, 2014; IPCC Working Group II, 2022; Pereira et al., 2012). These changes result in modified species' selective landscapes, diversity loss (genetic, specific and functional), changes in body sizes and population sizes, changes in communities' structure and dynamics, and ultimately changes in ecosystems' architecture and functioning (Pereira et al., 2012). However, our current knowledge of terrestrial and marine ecosystems only represents approximately 14 and 9 % of the real extant biodiversity, respectively (Mora et al., 2011). With over 31,000 known species currently under threat of extinction (IUCN, 2020), including many apex predators (Estes et al., 2011), the current scale and speed of biodiversity loss supports the idea that the ongoing biodiversity crisis is in fact Earth's sixth mass extinction (Barnosky et al., 2011).

Among Earth's ecosystems, marine biomes are the richest in terms of phylogenetic diversity (Rupert et al., 2003; Salazar and Sunagawa, 2017; Stal and Cretoiu, 2016), and most likely functional diversity (Mouillot et al., 2013). However, our ability to explain the mechanisms driving current biodiversity patterns, as well as predict future losses, is limited by important gaps in our critical understanding of how marine systems function. Consequently, we are faced with the challenge of finding approaches (observational, experimental, theoretical) that can integrate the complexity of marine biotic systems. Several tools and techniques are presently used to describe the patterns and dynamics of biotic systems' responses to environmental changes: e.g., field samplings and observations, in situ and laboratory manipulative experiments, omics approaches and ecological modelling. However, these tools have not been comprehensively integrated to push our understanding of the ecology, development, behaviour, physiology and evolution of biotic systems. Integrating different approaches is now relevant when dealing with multiple environmental stressors, with over 97 % of marine ecosystems being impacted by more than one stressor (Bopp et al., 2013; Halpern et al., 2015). Consequently, predicting biotic responses to multiple ocean change stressors becomes increasingly complex due to the emergence of synergistic and antagonistic effects (Côté et al., 2016; Piggott et al., 2015). In addition, studies investigating global change impacts on biodiversity need to consider shifts in ecosystem functions and services, climatic feedbacks, and societal responses. Such studies will enable conservation practitioners to be in the position to make better-informed and more impactful decisions to implement sustainable practices in the marine environment. In this context, climate-smart (or more broadly: global change-smart) conservation is a relevant concept, defined as "the intentional and deliberate consideration of climate change in natural resource management, realized through adopting forward-looking goals and explicitly linking strategies to key climate impacts and vulnerabilities" (Stein et al., 2014). Such concept can be expanded to include all levels of global change, and not just climate change. Ultimately, it is imperative we develop adaptation strategies that are robust to different degrees of global change uncertainties, interrelate human actions to ecosystem impacts, and consider vast landscape and temporal contexts when projecting changes. To do so, the creation of toolboxes exploiting the many advantages provided by recent advances in multiple fields of research (including biology, oceanography, biogeochemistry, bioinformatics and mathematics) is much needed. This calls for "big data" scientific innovations and the integration of multiple levels of biological organization: truly "from genes to ecosystems".

The aim of our work is threefold: first, identify current challenges in ocean data availability and usability; second, showcase why multilayer biological networks represent the best integrative approach to tackle these challenges; and third, identify the remaining knowledge / translation gaps to fill, to enable a more widespread application of multilayer biological networks, aiming to support the implementation of global change-smart conservation strategies for marine biodiversity.

2. Current challenges in ocean data availability and usability

The path for building a framework to predict the responses of marine ecosystems to global changes, whilst comprehensively dealing with the complexities of natural ecological systems, is fraught with challenges. First, if we are to accurately predict global change impacts on marine ecosystems, we need to improve the quality and speed at which data is collected and processed. For example, up to date, only 5 % of the ocean has been well explored, with another 10 % sparsely explored (Santoro et al., 2022). This means that a substantial part of the ocean is still uncharted. In this context, the development of ocean monitoring technology, namely autonomous devices for ocean measurements, e.g. the OceanGliders project (see Testor et al., 2019), will enable us to study remote habitats and increase data resolution on both the spatial and temporal scale. Furthermore, biological data collection and conservation efforts have been biased toward vertebrate species (particularly in terrestrial ecosystems) (Caldwell et al., 2024), overlooking the fact that macrophyte and invertebrate biodiversity and biomass are major drivers of ecosystem engineering processes and services, particularly in the marine environment (Cardoso et al., 2011; Eisenhauer et al., 2019; Prather et al., 2013). We emphasize the importance of collecting both field and experimental data and do so whilst standardizing operation procedures and ensuring data normalization to guarantee that datasets are of high quality and inter-comparable (see for example Benson et al., 2021).

Still, the most prominent issue with regards to the available data is that of the "tyranny of scales" (Gross and Green, 2017). This is the mismatch between the spatial (global vs. regional vs. local) and temporal (seconds vs. days vs. years) scales of relevant biological, ecological and oceanographic processes, that greatly limit our ability to reconcile management decisions. While tools such as environmental data projections and global species distribution models offer the ability for synthesis and integration of different scales, they consider only species' average responses to environmental variables (Vetter et al., 2015). Yet, the magnitude of environmental change is predicted to be spatially heterogeneous, and its impact on biodiversity will be governed by a suite of processes simultaneously acting at the local and regional scale (Helmuth et al., 2014; Wethey et al., 2011; Woodin et al., 2013). Therefore, local and regional models (including climate change models, species distribution models, population dynamics models, mechanistic or physiological models) will provide useful outputs to inform marine conservation strategies (see Rilov et al., 2019). However, such models do not integrate or allow interpretation of multiple levels of environmental and biological complexity. In fact, each level has its own type of data, with inherently different issues, uncertainties, units and analytical requirements. Adding to these challenges, a lack of central repositories, standardization of metadata and data formats, unified workflows, interoperability between software and the scarcity of marine-specific bioinformatics and modelling tools, prevents us to generate a coherent overview of global change impacts on marine ecosystems (Misra et al., 2019; Pinu et al., 2019). The growing environmental data science movement among marine scientists is currently addressing these needs for biodiversity data (e.g. OBIS, GBIF and WORMs as central repositories, Darwin Core as standard data format). However, much work is still needed when it comes to other types of marine data (e.g. physiological, molecular).

To tackle these challenges, we focus our attention on *Network Science* (i.e., defined as "the study of network representations of physical, biological, and social phenomena leading to predictive models of these phenomena", (Garcia-Robledo et al., 2016), as a way to connect evidence across different layers of the environmental, biological and ecological, as well as socio-economic hierarchies. We explain how this

will foster the utilization of an "environmental-biological systems synthesis" to face the current ongoing environmental and biodiversity crisis.

3. Global change risk assessment: toward the development of multilayer integrative approaches

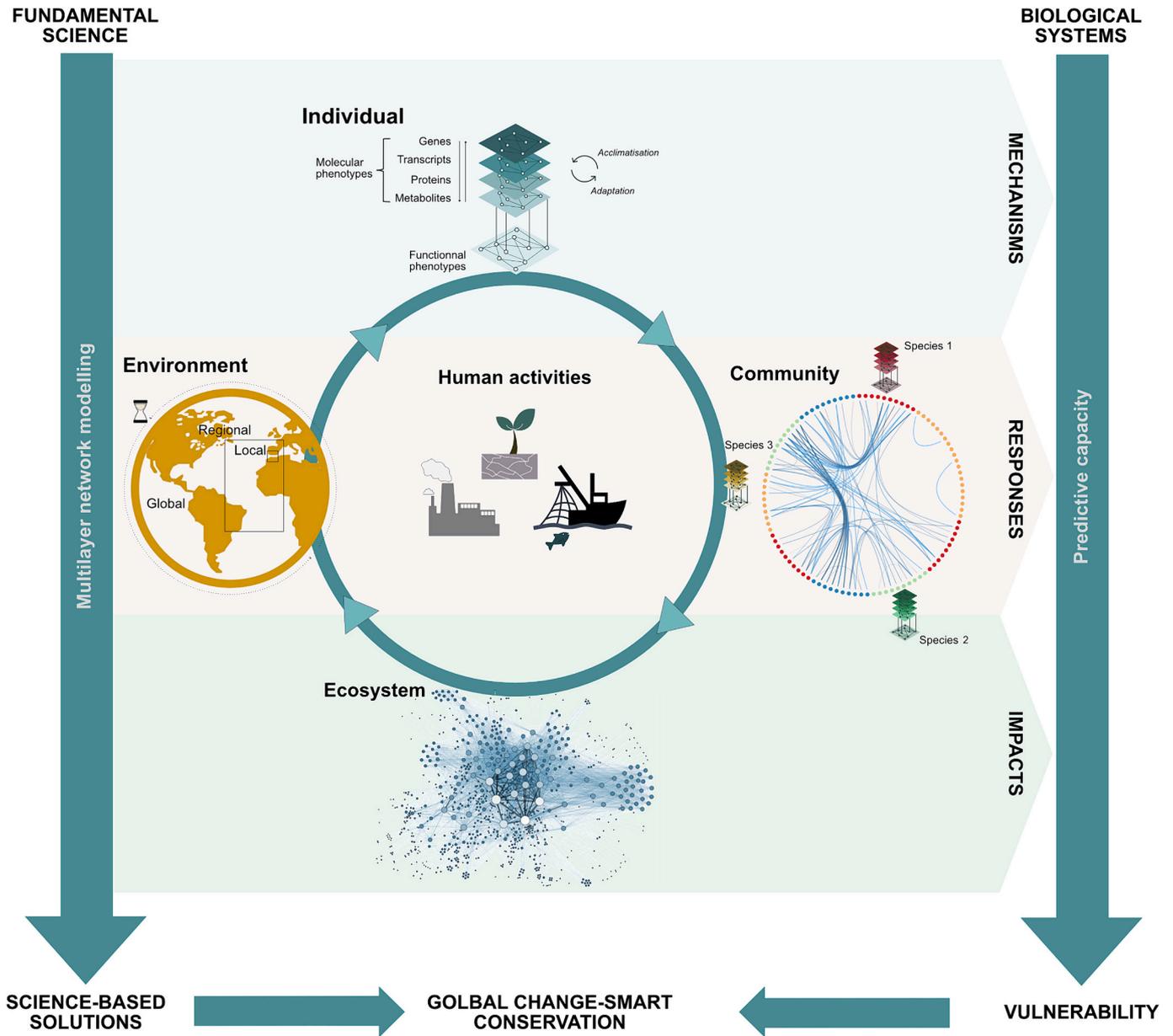We propose the utilization of an integrative framework, that pushes

Fig. 1. Environmental-biological systems synthesis. Proposed framework for global change research on marine ecosystems to inform current management practices, by promoting multilayer biological networks to support smart conservation strategies. Multiple stressors act individually or together on marine ecosystems at variable spatial-temporal scales. The level at which optimal resolution of these scales can be found is key to establish effective ocean observatories and modelling approaches to project future global changes impacts on biodiversity. Data collection along the different dimensions of environmental-biological axis (e.g., organisms' responses, species adaptation, ecosystem roles and services), as well as the socio-economic axis (human activities and associated social, cultural, political, and economic aspects) is paramount to this goal. Within the environmental-biological axis, the critical understanding of three main framework components: i) physiological mechanisms, ii) community responses and feedback mechanisms and iii) ecosystem responses, collectively contribute to define our predictive capacity to assess vulnerability (and risk) levels in different biogeographical contexts. At the level of individual organisms, the discovery of physiological mechanisms depends on combining high-throughput approaches (e.g., multi-omics) that allow us to integrate information on the molecular make-up and regulation of multiple organismal compartments: from genes to metabolites. From here, we can identify functional phenotypes and statistically infer on the capacity of marine organisms for acclimatization, persistence and rates of adaptive evolution. The variability in organisms' physiological mechanisms and consequent tolerance of global changes is reflected into changes at the species abundance level. This will further scale-up to community and ecosystem levels, as species abundance defines the intensity, direction, and feedback loops of species interactions. This can lead to dynamic changes in various community and ecosystem dimensions: including structure, diversity, heterogeneity, complexity and services. Feedback loops resulting from these changes can, in turn, also act as mechanisms, changing individuals' development, behaviour and physiology. Therefore, the path from fundamental science to science-based solutions relies on the integration of these different data and information sources through multilayer network modelling. Only through the combination of the two ends of the spectrum – i.e., vulnerability assessments and science-based solutions – we can achieve the overarching goal of global change-smart conservation, governance, and policies.

forward the concept of an environmental-biological systems synthesis (Fig. 1) between organismal, ecological and environmental data, providing a working framework for reproducible and evidence-based decision making (sensu Wei et al., 2015). This framework can include different kinds of evidence, such as whole-organism and ecological data (incl. Field and common garden experiments, from molecules to ecosystems), and also include socio-ecological and socio-economic data, thus scaling up to socio-ecological systems (SES - *sensu* Mascia et al., 2017; Virapongse et al., 2016).

One avenue for implementing an integrative multilayer biological network approach in marine research is to bring *Complexity Science* (i.e. the study of complex systems and their non-trivial global structures and behaviours, see Braithwaite et al., 2018; Lewison et al., 2018) into marine physiology, ecology and conservation (Heleno et al., 2014;

Manzoni et al., 2018). One branch of Complexity Science, termed Network Science, is especially useful in this context as it proposes that biological systems can be modelled as interconnected networks, forming multi-layered structures that behave and evolve together, according to their interdependency and dynamic processes (Aleta and Moreno, 2019). Firstly, to identify emergent properties of complex biological systems, we need to characterize each layer (of the system), namely its constituents (nodes) and their interactions (edges) (Gross and Green, 2017). As we combine the networks obtained from each layer, which can represent different levels of information (e.g., molecular, organismal, ecosystemic) or the same information across time or space, we obtain a multilayer network with enhanced complexity (Fig. 2). To understand its dynamics, we need to shortlist the set of driver nodes that regulate the multilayer system in response to the external environment (Zheng et al.,
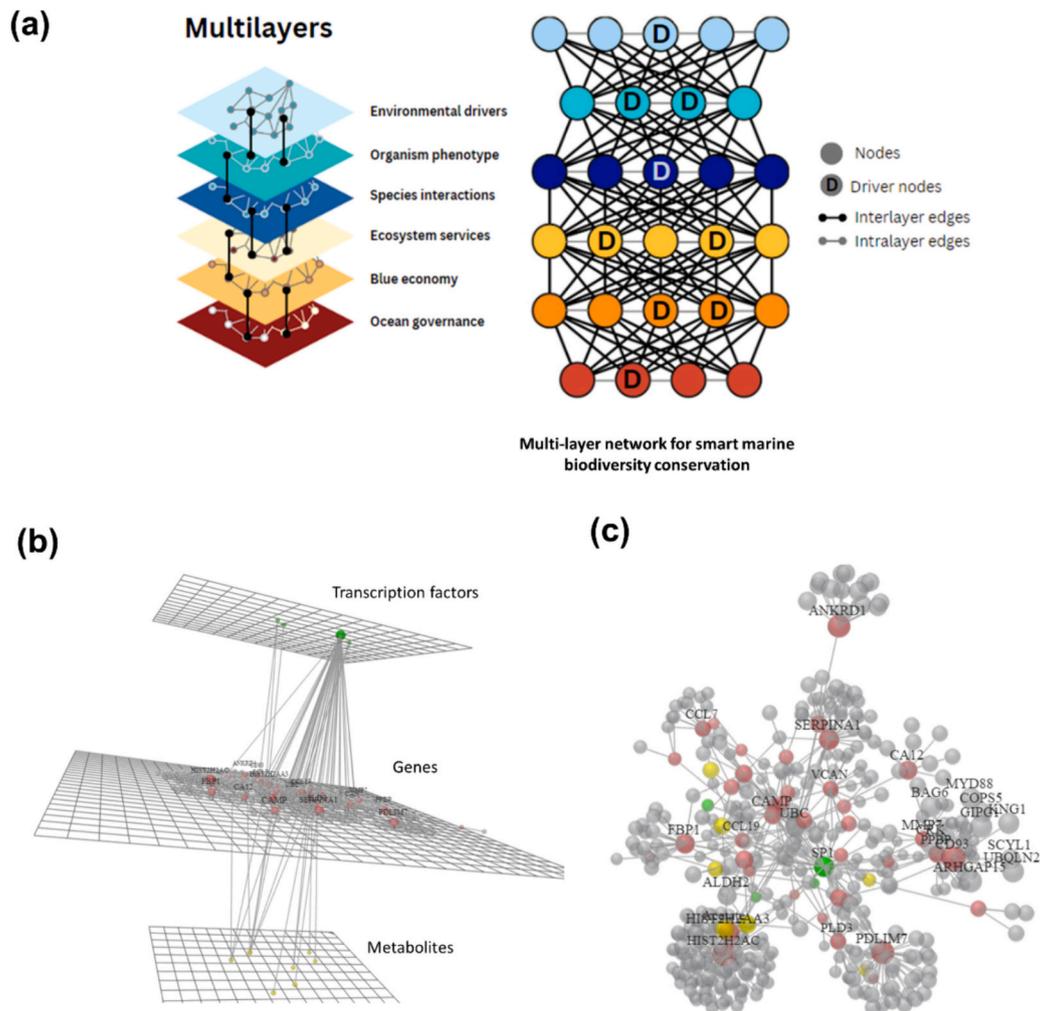

Fig. 2. Multilayer networks. (a) Schematic representation of a multilayer network. Each layer can represent (i) a specific level or type of information or (ii) the same type of information across time or space. Each layer is composed of interconnected nodes that represent relationships between entities e.g., co-regulation of environmental drivers; chemical reactions between molecules; interactions between individuals – competition, social interactions, mating; or between species – trophic relations, competition; co-dependency of human activities. Interlayer connections relate to the type of interactions between layers, and these could represent metabolic regulation to produce a phenotype, process feedback, governance actions that regulate human activities, etc. When all layers are connected and modelled, multilayer-network driver nodes can be unravelled. These are the nodes that drive the structure and dynamics of the network and could be potential targets for practical applications: e.g., molecules that respond to environmental change that could act as biomarkers; species or populations to target for conservation; specific environmental parameters for monitoring; specific human activities with a large impact in the ecosystem. This multi-level type of network usually entails processes that cascade through the different levels. The identification of these processes represents one of the greatest advantages of multilayer network analyses, as it provides a mechanistic understanding of up- and down-scaling of biological, ecological or socio-economic phenomena, increasing our ability to predict responses of biological systems to global changes. (b) Example of a multilayer human molecular interaction network (interactome network) produced in OmicsNet (Zhou and Xia, 2019) using the software's example dataset, composed of six transcription factors (coloured as green nodes), 48 genes (coloured as red nodes and immediate interacting partners in grey), 33 metabolites (coloured as yellow). We defined protein-protein interactions as the primary network (extracted from gene information) and then added transcription factors and metabolites targeting nodes in the primary network. The graph layout is "perspective". (c) The same network as in (b), represented using the "standard" layout.

2019). This can be achieved by graph theory, computer science and statistical inference (Aleta and Moreno, 2019). Then, the multiple levels of information are connected using advanced statistical methods: e.g., Bayesian hierarchical modelling, multi-block regression, neural networks, unsupervised machine learning (e.g. Wu et al., 2019).

To better understand the potential applications of this framework, we provide six examples of multilayer networks applied to conservation ecology and evolution (Fig. 3). Three of these examples come from the marine realm, showcasing that the use of a multilayer framework is already being used, although very limitedly; other three examples come
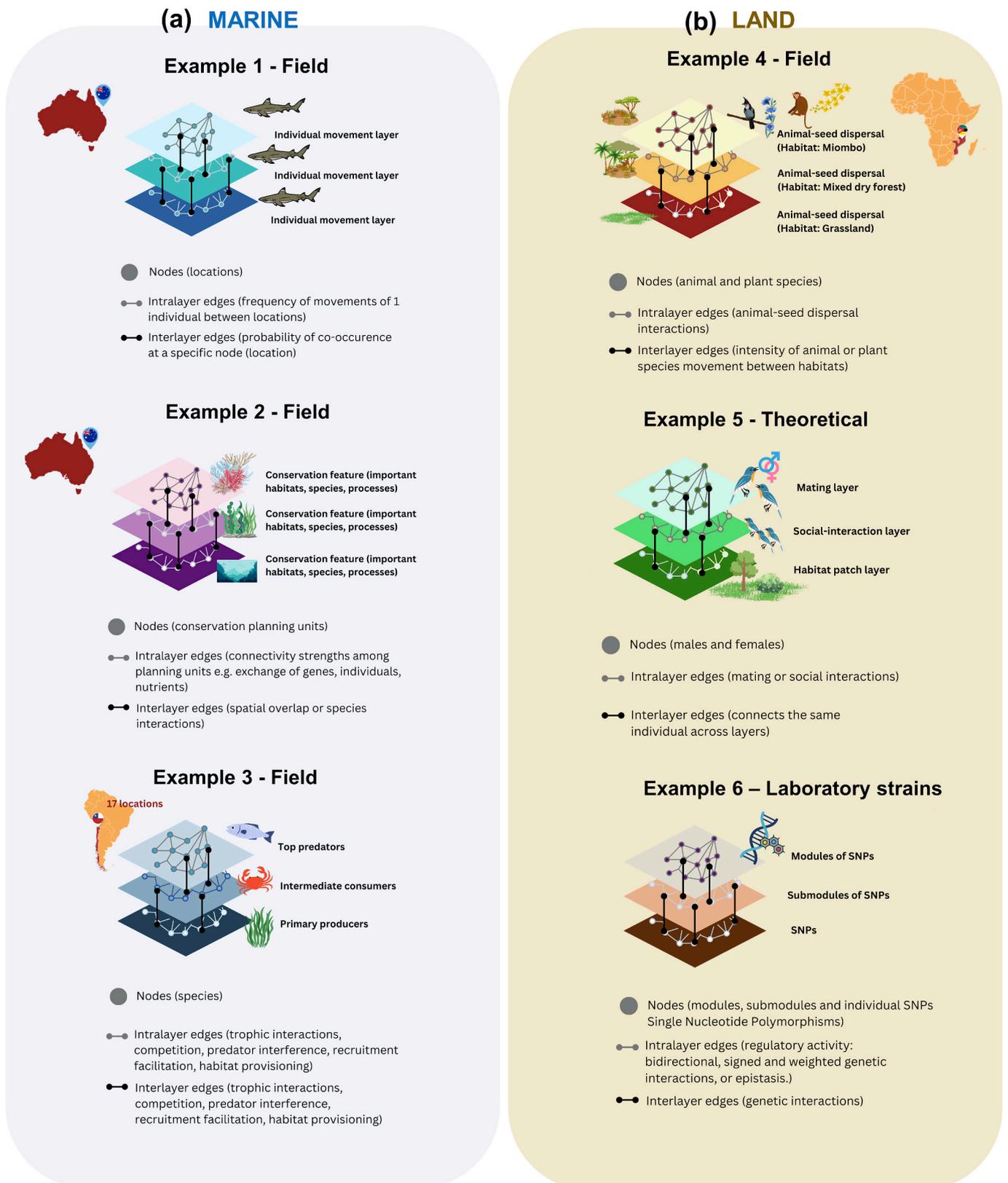

Fig. 3. Examples of multilayer networks applied to conservation ecology and evolution.

from the terrestrial realm, to showcase best practice in this emerging discipline, and discuss how lessons learned from different systems can be modified and applied to analogous marine applications:

1. Multilayer networks in shark ecology in the Great Barrier Reef (Mourier et al., 2019): in this study, the authors use multilayer networks to study shark movement in the reef. The authors use passive remote sensors to track individual shark movements, which will form individual movement networks: i.e., (layers). Then, the layers are connected in a multilayer network by using the probabilities of social interactions as interlayer edges. This approach enables the remote study of spatial use by species in the wild and provides relevant information for applied ecology and conservation.

2. Multilayer networks in Protected Area design and its application to the Great Barrier Reef (Daigle et al., 2020): in this study, the authors developed a conservation planning tool, Marxan Connect, which is designed to facilitate the inclusion of ecological connectivity in protected area network planning, and applied it to the Great Barrier Reef to demonstrate its workflow with minimal data requirements. This tool finds cost effective selections of "planning units" that meet "conservation targets". For example, spatial grid cells include a percentage of a "conservation feature" such as the critical habitat of a species at risk. Additionally, a suitable spatial arrangement (e.g., edge to area ratio) should be based on spatial dependencies (e.g., shared planning unit boundaries). Ecological connectivity can be included in both the conservation targets or the spatial dependencies. In summary, each layer represents a conservation feature (e.g., important habitat, species or process), composed of several planning units (nodes) with intralayer edges. These edges represent connectivity strengths among planning units: e.g. the exchange of genes, individuals, or ecosystem connectivity. In the ecosystem case, the strength of the edges represents the exchange of nutrients or energy among planning units. Users can choose (1) to include a single connectivity matrix to be used as a spatial dependency, which will minimize the number/strength of edges that flow out of the selected planning units (i.e., spillover) and/or (2) one or more connectivity matrices to be used as a conservation feature for which the tool uses network theory metrics (e.g. centrality) to identify a discrete set of the 'best' planning units (e.g. most connected) to be targeted for selection in protected area planning. The only connection among the network layers, if there are more than one, is their spatial overlap. Other possible connections among the network layers (e.g., species interactions) are not considered by the tool. Overall, because of the inclusion of ecological connectivity, the solutions provided by the tool are more likely to support persistent and resilient metapopulations and provide better protection for biodiversity. Similar to this example, other studies have also used networks for analysing seascape connectivity in Hawaiian coral reefs, helping to define conservation priorities (Treml and Kool, 2018).

3. Multilayer networks in marine intertidal communities (Lurgi et al., 2020): the authors aimed at unravelling the spatial variation of multiplex ecological networks in marine intertidal communities, considering trophic and non-trophic interactions. For that, the authors gathered species composition data and considered three types of ecological interactions across a large geographic scale (17 locations across 970 km), while finding the main environmental drivers explaining network organization and geographical variation. The nodes in the network represent species and the three types of interactions constitute the edges, organised into three layers, representing trophic, non-trophic negative (e.g. competition or predator interference) and non-trophic positive interactions (e.g. recruitment facilitation, habitat provisioning), resulting in a metaweb for each location. The authors conclude that environmental drivers (e.g. temperature, upwelling) modulated species richness and species interactions, mediating structural properties of the networks. Non-

trophic negative interactions are particularly sensitive to spatial environmental gradients when compared to trophic and non-trophic positive interactions. This approach may provide key information to predict the responses of marine communities to climate change. Complementary to this study, Mendonça and Vinagre (2023) analyse the temporal variation in complex trophic networks over a tidal cycle, highlighting that high tides, while adding new species, do not add complexity to intertidal food webs. However, pools created during low tide add species diversity and network complexity. They also conclude that disturbance can travel fast through food webs via predator-prey links, a key aspect for conservation of intertidal rocky reef communities.

4. Multilayer networks in seed dispersal interactions in the Gorongosa National Park (Timóteo et al., 2018): in this study, the authors represent animal dispersers and plant species with dispersed seeds as the nodes in the network. These nodes are connected via intralayer edges: i.e., animal-seed dispersal interactions. This information is then adapted to construct different layers, which represent the different habitats of the Gorongosa park. The connections of nodes between the layers (i.e., interlayer edges) represent movements of animals or plant species between the habitats: the intensity of movements can be used to define the intensity of habitat coupling and hence the strength of the interlayer edges. After the estimation of network statistics, the authors concluded that seed-dispersal patterns are determined by dispersers that span across habitats and thus link the different landscapes, suggesting that habitat connectivity is key to determine the spatial structure of Gorongosa park. The authors conclude by stating that this information is key in defining conservation strategies for the park. A clear parallel between seed dispersal in terrestrial plants via animal dispersers and marine pelagic larvae dispersal via ocean currents can be made, and the concepts and framework developed here modified and transposed to define conservation strategies for marine parks.

5. Multilayer networks in animal behaviour (Silk et al., 2018): the authors advocate the use of multilayer networks to study animal social behaviour and consequent eco-evolutionary patterns. For example, they propose a network with three layers: the top layer representing a mating network, composed of different coloured nodes (males and females), which are connected (intralayer edges) based on mating information (either observational or genetics). Then, a middle layer represents social interactions (which are the intralayer edges) between the individuals (nodes), while the bottom layer represents connected habitat patches. Interlayer edges between the top (mating) and middle (social interaction) layers connect an individual to itself while interlayer edges between the middle and bottom (habitat patches) layers connect individuals to habitats visited. Based on this multilayer network approach, links can be established between animal behaviour and habitat use, providing relevant information to wildlife managers. This approach stems particularly from study on social terrestrial mammals/birds species and could help develop multilayer networks to study the social behaviour, consequent eco-evolutionary patterns and help enhance conservation in social marine mammals/birds, but also social ectotherms: such as fish and cephalopods.

6. Multilayer interactome networks in organism plasticity and evolution (Yang et al., 2021): the authors aimed at unravelling the genetic mechanisms underlying plastic responses in growth of a bacteria (*Staphylococcus aureus*) when exposed to an abiotic stress (antibiotic exposure, namely vancomycin) and to a biotic factor (co-occurrence with other bacteria, namely *Escherichia coli*). Taking the example of antibiotic exposure, different genetic variants may underlie antibiotic resistance in *S. aureus*. Therefore, the authors perform a genome-wide association experiment to unravel Single Nucleotide Polymorphisms (SNPs) that can explain different phenotypic plasticity in bacterial growth in a vancomycin-containing or vancomycin-free media. Briefly, it is assumed that the effect of an

SNP can be associated to its own intrinsic capacity to modulate plasticity (independent effect) or an effect that results from regulation by other SNPs (dependent effect). These independent effects (SNPs themselves) can be considered the nodes of a network while the edges are the dependent effects, indicating regulatory activity: bidirectional, signed and weighted genetic interactions, or epistasis. Then the authors consider that SNPs can be grouped into functional modules based on the similarity of their genetic effects on bacterial growth, and this modularity can be incorporated into a multilayer network. Briefly, the authors identify 14 modules of different sizes, which results in a 14-node genetic network explaining the plastic response of *S. aureus* to the antibiotic (first layer of the network). Then they subdivide each module into distinct submodules (second layer of the network) and continue the process until no further subdivisions can be detected. The interlayer edges also represent genetic interactions, and if we follow these edges from the top to the bottom layers, we will have the pathway of each gene determining phenotypic plasticity. This approach could also be applied to study marine organism plasticity and evolution, although genome wide association studies may not yet be possible in many species. Nevertheless, we could focus on species with whole genome sequencing available to take the first steps in building SNP networks or other molecular interactome networks: here *interactome* is defined as the set of molecular interactions that can occur between any type of molecule – nucleic acids, proteins, metabolites, lipids – defining the phenotype of a cell / tissue / organism (Luck et al., 2016).

From these examples, we can see how Network Science (see Boccaletti et al., 2014), enables us to integrate information into tractable models that classify the groups of interactions according to their characteristics, improving predictability of system processes (e.g. Aleta and Moreno, 2019). The detection of connected components in multilayer networks, their controllability properties (Bianconi, 2018; Liu et al., 2011) and top-down boundaries (from human activities, environmental conditions, ecosystem type, organism, tissue to cell structure) are key to understand system tolerance and resilience to disruptive events (Menichetti et al., 2016). For example, each network has a set of nodes that respond to specific signals and end up defining the final state of the networks; these are called driver nodes. These nodes display a hub effect and discovering them, as well as the input signals to which they respond to, will allow us to control the network (Bianconi, 2018; Liu et al., 2011).

To apply this network science-based approach in the context of climate and global change impacts on marine biodiversity, we propose, as *first step to acquire a better understanding and relevant data on links between genotypes, molecular (omics) and functional phenotypes at the individual level*. This individual level data will allow us to produce robust predictions about cellular and physiological mechanisms underlying life-history traits and fitness outcomes across populations and taxa. This data can be obtained through metapopulation field assessments (particularly along natural environmental and geographical gradients) and laboratory experimentation, providing a map of genes' and proteins' interactome networks underlying sensitivity or tolerance to environmental change. For this, omics tools can provide a comprehensive account of the molecular functioning of an organism's cell, which will allow in turn to identify causative molecular changes underlying adapted vs. mal-adapted phenotypes.

*As a second step, the establishment of cause-effect relationships from lower (*i.e.*, the cell and individuals) to higher (*i.e.*, populations, metapopulations and ecosystems) levels of biological organization can be achieved by linking individuals' cell physiology to whole-organisms' physiology*. More specifically, here we advocate to move toward the use of multivariate correlative approaches that are able to integrate multi-omics dataset to multiple whole-organism's traits dataset (using available network analyses and software). This way, we will be able to move beyond univariate correlative approaches that relate semi-quantitatively or quantitatively, single omics data to a whole-organism single trait (Calosi et al., 2017;

Madeira et al., 2017). Following, whole-organisms' physiology can be connected to populations' demography and distribution (Pörtner and Knust, 2007), and these together to ecological and ecosystems' processes: e.g. community dynamics, primary production, trophic relationships, carbon storage capacity, etc. Once network models are applied to the data, fragile nodes in ecosystem and biological networks can be identified. These nodes can represent molecules in one layer (useful as biomarkers) and individuals or populations in other layers, which are direct targets of conservation actions, via different approaches: e.g., marine protected areas, assisted migration and assisted evolution. Multilayer networks have already proven to be powerful tools in phenotype prediction and modelling of cellular processes (Zheng et al., 2019), disease diagnostics (Guillon et al., 2017; Rai et al., 2017), animal epidemiology (Kinsley et al., 2020), the study of ecological patterns (Albouy et al., 2019; Hutchinson et al., 2019; Mello et al., 2019; Pilosof et al., 2017; Timóteo et al., 2018) and animal behaviour (Silk et al., 2018), as well as in the assessment of the socio-ecological fit of conservation strategies (Alexander et al., 2017; Alexander and Armitage, 2015). However, the link between environment, metabolism, physiological processes and ecosystem structure and dynamics has not yet been fully explored, nor applied in marine conservation. The application of multilayer networks in this context will allow us to: (i) connect quantitatively top-down (community/species interactions exert feedback on individuals and their physiology) with bottom-up processes (individual phenotypes define populations and communities) and explore how their relationships, interactions and feedback change across space and time. This will allow us to understand ecosystems responses to global change drivers, and (ii) identify biological functions' bottlenecks (driver nodes of a network) at different levels of the biological hierarchy, in response to single and multi-stressor horizons. Overall, these multilayer network approaches will allow biological patterns to be derived from multi-scale information, across space and time, while finding critical thresholds (tipping points) of tolerance and resilience for populations and ecosystems (*sensu* Asseng et al., 2021; Carrier-Belleau et al., 2023; Carrier-Belleau et al., 2022; Spake et al., 2022).

The interactions among these different levels of information and their sensitivity to global changes ultimately define current and future biodiversity levels, and their relationship to ecosystem functioning and services. These aspects should all be integrated into prognostic risk assessments and ecosystem management planning (Dee et al., 2017; Mace et al., 2012). However, to successfully implement a multilayer assessment of biodiversity, we need to improve:

  (i) our understanding of molecular biological systems and their relationship with performance and fitness,

 (ii) standardize data collection efforts and methodology to maximise data comparability; the collected data needs to be made publicly available, and the need and benefits of inter-calibration exercises should be emphasized for broad scale applications: for example, as for the implementation of the EU's Water Framework Directive.

(iii) integrate multiple sources of variation into baseline models for more realistic forecasting,

(iv) foster interdisciplinary collaboration with mathematicians and modellers

 (v) keep improving multilayer network visualization and develop increasingly friendly tools to engage with these complex networks.

We also highlight that, whereas we mostly focus our attention on metazoan communities due to their interest in marine conservation, this framework can be applied to unicellular and multicellular organisms alike. For example, network approaches should also be used to study highly diverse communities of marine protists and bacterioplankton, which drive a substantial part of primary production and nutrient cycling in the ocean (e.g. Bunse and Pinhassi, 2017). Here too we limit our overview of ocean processes to that of environmental drivers, rather

than oceanography *per se*, which considers Lagrangian processes embedded in 3D circulation (Sebille et al., 2018). The latter case implies biophysical interactions in a moving fluid, representing a dynamic system where nodes and edges may rapidly appear, disappear or stretch/shrink in their interaction strengths. Such dynamism over the time-space continuum can be attributed to any natural system and could be further explored in marine network science (see for example Mendonça et al., 2022).

4. Gaps in critical understanding and translation of multilayer data to inform conservation strategies

Adaptive conservation actions for biodiversity, which also consider socio-economic interests, will have a far greater impact if designed based on information generated from targeted multilayer research efforts. Such approach will help strengthen the nexus science-policy/management as highlighted in examples above (shark movement in the Great Barrier Reef, seed dispersal in Gorongosa National Park and Marxan Connect tool in Protected Area design). For better knowledge mobilisation, scientists and stakeholders can co-create analytical frameworks and tools purposefully designed to respond to specific conservation needs. Some methods that can help achieving this goal include participatory frameworks like knowledge-to-action (K2A), co-design and production, policy-informed research or intersectoral collaborations supported by impactful dissemination (Cvitanovic et al., 2015; Sudsawad, 2007). Given the fast pace of global change, and the urgency for adaptive marine conservation strategies, it is essential that the development of theory, tools, technology, and data collection is accelerated. A wider application of multilayer network science will be a crucial and innovative step to support the maintenance of ecosystem services, food security, and human health in a changing world. It will also enable the development of theory and improve our critical understanding of both environmental-biological and related socio-economic systems.

Below, we evaluate our ability to adopt a multilayer network approach to support marine conservation, illustrated through examples that can either be adopted immediately, are ready to be transferred, or require further development but should become working priorities.

4.1. Immediate adoption

- Integration of existing information networks. Information networks can connect existing evidence at various levels (oceanographic, biosphere, societal and economic) to support the development of management and conservation activities (Canonico et al., 2019; Gonzalez et al., 2023): e.g., the Global Omics Observatory Network (GLOMICON), Global Biodiversity Information Facility (GBIF), Marine Biodiversity Observation Network (MBON), Global Ocean Observing System (GOOS), Global Ocean Acidification Observing Network (GOA-ON). Now, information at an ecological level such as species abundance, species interactions and habitat connectivity can be used in multilayer network modelling, as seen in examples above.
- Implement multilayer networks in the design of marine protected areas (MPA) considering multi-stressor contexts. Currently, we are already aware of the range of multi-stressors impacting marine coastal ecosystems (Halpern et al., 2015; Côté et al., 2016), with documented effects on abundance, survival, biomass or diversity (Breitburg and Reidel, 2013; Reusch et al., 2018; Smith et al., 2023). Interactions between stressors can result in non-linear biotic responses, including synergistic or antagonistic responses, which are often overlooked in marine conservation efforts. Patterns of habitat connectivity, relationships between ecological components, ecosystem functions and services provided to society under multi-stressor contexts are all essential features to help designing MPA. Given UN's goal to protect 30 % of the ocean by 2030, we advocate the application of multilayer network analyses to sensibly improve

the management of coastal habitats and more precisely define multi-stressor impacts on planning units and their connectivity, species interaction networks or socio-ecological networks (e.g. see for example Beauchesne et al., 2021; De Juan et al., 2023). By incorporating this information into MPA, we will be able to monitor and anticipate global change related risks and account for them on biodiversity protection efforts. While data may still be missing for several information layers (particularly at the molecular and physiological level), this should not stop scientists and practitioners from running models with the data that already exists. In the meantime, we should work on acquiring the data on missing layers, improving and refining the networks as new information becomes available.

- Essential Variables and Open DataCube. A harmonized real-time observation system should be created at a global level to store and share data: including changes in biodiversity (incl. Specific, genetic and functional biodiversity), physicochemical parameters, ecosystems functions, and their linkages, taking example from or building upon existing Biodiversity Observation Networks (BON): such as the Marine Biodiversity Observation Networks (MBON, Duffy et al., 2013, Chavez et al., 2021, Benson et al., 2021) and the Omics Observation Network (Omic BON, Meyer et al., 2023), both associated to the Group on Earth Observation's Biodiversity Observation Network (Canonico et al., 2019). We propose that the established set of *Essential Biodiversity Variables* (Pereira et al., 2013) be monitored, including with taxonomical, phylogenetic and functional diversity metrics, also genetic, molecular and whole-organism phenotypes diversity metrics. We also urge to do so at the individual level, as the ultimate unit of selection, instead of stopping at the species level. Further, we propose that *Essential Environmental and Socio-Economic Variables*, as well as *Essential Ecosystem Services* (e.g. Karp et al., 2015) are also defined and recorded in a coordinated fashion, following FAIR data principles. All data should be made available on an Open DataCube, accessible to scientists and stakeholders worldwide.

4.2. Transformation required

- Annotation of genes, proteins and metabolites across the (marine) tree of life. The lack of functional understanding about genes, proteins and metabolites in marine species is a great bottleneck for the use of these molecules in the investigation of phenotypic-fitness responses to the ongoing environmental change. Increasing the annotation efforts, the available tools and current computational ability will critically enhance our understanding of eco-evolutionary processes, particularly in the marine realm where such work lag historically behind. Increasing our understanding of the role of epigenetics in modulating phenotypic responses will also complement these efforts and add another layer of information to multilayer networks. Incorporating an "all-taxa all-layers response inventory" obtained through the characterization of molecular-functional phenotypes in marine organisms across entire ecosystems will multiply the efficiency of this framework. While a specific roadmap for connecting lower layers (from the molecular to the organismal level) is inherently dependent on data type, quality and quantity, this task could be achieved via several pathways, including i) the analysis of co-expression networks of genes, proteins and metabolites and their correlation to observed phenotypes, ii) association of genetic variants with phenotypes, and iii) association of plasticity levels with monogenic or polygenic traits. Interesting examples from the medical sciences could steer future implementation in other research fields (e.g. Núñez-Carpintero et al., 2024; Hammoud and Kramer, 2020).
- Development of user-friendly analytical platforms and software to carry out complex Networks-of-Networks analyses accessible to all scientists. The emerging field of NetoNets (D'Agostino and Scala, 2014) – i.e. the creation of networks - aims to provide a new

integrated vision on vulnerabilities and system behaviours: including biological, financial and social systems. The application of the NetoNets framework will bring novel solutions to real-life problems in conservation: for example, better describing emergent properties and organization of systems when compared to classical approaches and providing greater insight into cause-effect relationships in system functioning.

4.3. Further development

- Maintenance of compatibility between multiple systems, co-construction and inclusiveness. The rise of a sustainable model for the future needs to be shaped in a way that stabilizes the merged systems (i.e. ecological, social, economic, political and institutional) that form an interactive super system (Alexander et al., 2017; Alexander and Armitage, 2015; Yolles, 2018). We need to recognise that perceptions and implications of global changes are different for distinctive communities. Accordingly, we need to globally harmonise biodiversity conservation goals but allow for flexible strategies to identify and protect key resources. This is crucial to maintain livelihoods and define the most appropriate local management strategies. We need to facilitate the co-construction processes, which will help integrating the knowledge of researchers, decision makers and stakeholders from early on in research and conservation programs and actions. This will enable us to build a toolbox that accounts for different types of information with different spatio-temporal scales within different environmental-biological-socio-economic contexts. Ultimately, the key to success relies on inclusiveness: embracing diversity, working on our capacity for learning and self-reorganizing, and recognizing that trust and collective actions are the pillars upon which to build ecosystems and social resilience.

5. Future opportunities and challenges

Rebuilding marine life is a Grand Challenge for humanity (Duarte et al., 2020). In this sense, developing multilayer biological networks to support global change-smart marine conservation strategies is key to promote the sustainable use of marine resources in a changing ocean. Multilayer networks represent a cutting-edge tool to improve our understanding of emerging properties of biological systems exposed simultaneously to multiple drivers, and consequently improve our predictive ability for the emergence of synergistic and antagonistic responses (of organisms to ecosystems) to complex environmental conditions (e.g., Côté et al., 2016; Piggott et al., 2015). Multilayer networks are highly flexible in configuration and can be customized on a case-by-case basis, being applicable to a wide range of research fields. By integrating different levels of information using Network Science, we will elucidate biotic systems' functioning and vulnerability, like it has not been possible to date. This will endorse innovative solutions, new think-boxes and paradigm shifts in marine ecology and conservation. However, there are still limits to this approach that need to be urgently addressed by multidisciplinary research consortia. For example, how to define which entities are the nodes, what each layer represents, and which type of interactions define intra- and interlayer edges. Moreover, can these interactions be defined and quantified (e.g. upstream-downstream processes, feedback systems, controllers)? How to deal with the issue of the "tyranny of scales" in the datasets? How to deal with missing data, across different layers of a NetoNet? Moreover, one must consider the complexity and computational costs of running multilayer networks, the need for training datasets and the need for highly qualified personnel for implementation. Issues such as overfitting or underfitting of the data also need to be ascertained. The examples provided in this paper confirm the usefulness of multilayer networks in ecology, evolution and conservation, but for their widespread application, we need to resolve these questions and develop user-friendly tools.

This is a crucial step to enable scientists and practitioners to extract relevant response patterns from big data analyses. The widespread application of the described framework should be a research priority for the next decade as it will open new avenues for evidence-based conservation actions, the smart use of limited resources and the attraction of funds for ocean protection. While big data integration is widely developed in the medical sciences (Dash et al., 2019; Ristevski and Chen, 2018), commerce and smart cities (Blair et al., 2019), environmental sciences are clearly lagging behind, at great cost for biodiversity and natural resources. We must urgently define a safe operating space for humanity within the multidimensional seascape if we are to mitigate Earth's six mass extinction.

CRediT authorship contribution statement

Diana Madeira: Writing – review & editing; Writing – original draft, Visualization, Supervision, Methodology, Conceptualization. **Carolina Madeira:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Conceptualization. **Piero Calosi:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Fanny Vermandele:** Writing – review & editing, Writing – original draft. **Charlotte Carrier-Belleau:** Writing – review & editing, Writing – original draft, Visualization. **Aura Barria-Araya:** Writing – review & editing, Writing – original draft. **Remi Daigle:** Writing – review & editing, Writing – original draft. **Helen S. Findlay:** Writing – review & editing, Writing – original draft. **Timothée Poisot:** Writing – review & editing, Writing – original draft.

Declaration of competing interest

None.

Data availability

No data was used for the research described in the article.

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