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Regulation and maintenance ecosystem services in a coastal-marine continuum: Unravelling the underlying ecological structure and functioning

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A B S T R A C T

Understanding the ecological complexity underlying ecosystem services supply is essential to improve the practical application of the ecosystem services concept, enhance stakeholder understanding, and support effective ecosystem-based management. This study applied a theoretical network-based overview of the ecosystem services cascade framework, linking the different 'steps', from the ecological structure and functioning to ecosystem services and societal goods and benefits. Combining ecosystem models, information from the literature, and empirical data, the robustness of the ecological sub-system ecological functions supply underpinning the supply of regulation and maintenance ecosystem services was analyzed, at a coastal-marine interface of the northern coast of Portugal. The findings highlight the intricate relationships within the system ecological components that contribute to regulation and maintenance ecosystem services supply. The analysis shows that lower trophic levels (e.g. algae and macroalgae, macrophytes, macrozoobenthos or suprabenthic invertebrates) are key to directly sustaining function supply and the consequent regulation and maintenance ecosystem services, and phytoplankton and zooplankton the most important groups in indirectly support the ecological functioning in the region. Some ecological functions revealed a potential lack of resistance and resilience due to being supplied by one or a few functional groups, while most functions were supplied by various biota groups. The findings emphasize the significance of considering the different biota group relationships in management practices. This holistic approach allows managers and regulators to navigate the complexities in marine and coastal ecological systems that support its functioning and the provision of regulation and maintenance ecosystem services, and thus the provision of the other types of services and hence societal goods and benefits, to mitigate potential unaccounted or indirect pressures on system components.

1. Introduction

Human well-being depends on the natural assets and capital provided by ecosystems (Millennium Ecosystem Assessment, 2005), which comprise diverse biotic and abiotic components and their functions (Tett et al., 2013), structuring the ecological ecosystem (Harris and Defeo, 2022; Perschke et al., 2023). This structure generates Ecosystem Services (ES), and in turn, societal activities then obtain Societal Goods and Benefits (SGB), fulfilling the various needs and demands of society (Elliott, 2023; Elliott et al., 2017). However, human activities

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increasingly pressure ecosystems, particularly in marine and coastal areas (Halpern et al., 2019; Johnson et al., 2017). A key challenge is to balance our use of the benefits from ecosystems without compromising their resistance and resilience, productivity, and capacity to provide ES and SGB (Elliott and O'Higgins, 2020). The adoption of the ES concept and the application of the Ecosystem-based Approach and its operationalisation through Ecosystem-based Management aim to balance maintaining ecological status and sustainability, while accommodating the many human activities. However, there remains the need to enhance the operational implementation of these approaches and to unravel the ecosystem pathways to the generation of ES and SGB, particularly in marine areas (Galparsoro et al., 2021; Nahuelhual et al., 2020; Rodrigues et al., 2017). For instance, in the European Union (EU), initiatives such as the EU Marine Strategy Framework Directive (EU, 2008) and EU Maritime Spatial Planning Directive (EU, 2014) are legal instruments designed to maintain good environmental status, the integrity of marine ecosystems and the sustainable management of marine resources.

The ES cascade framework (Potschin-Young et al., 2018) conceptualizes the pathway from ecosystem components and processes to human well-being. Despite its widespread recognition, it is specifically highly contingent on site specific and assessment objectives (Potschin-Young et al., 2018). Nevertheless, knowledge gaps persist in understanding the connections between different steps of the cascade, particularly regarding quantifying relationships among ecological structure, biodiversity and functioning (Balvanera et al., 2016; Daam et al., 2019). These gaps pose challenges for stakeholders, fostering uncertainty and difficulty in grasping the concepts behind the ES approach, thereby complicating their implementation in managing marine and coastal ecosystems (Galparsoro et al., 2014; Nahuelhual et al., 2020). Despite this inherent complexity, which is challenging to disentangle, addressing these knowledge gaps is key for improving ES assessments, and promoting their application in management (La Notte et al., 2017; Notte et al., 2022). Specifically, better management requires a comprehensive view of the ecological connectivity within a particular system, an understanding the relationships between ecological structure and awareness that the provision of ES and SGB is necessary across multiple spatial scales. Hence a holistic view in management approaches is necessary (Elliott et al., 2020), to understand how various activities impact each of the different steps of the ES cascade and the environment, potentially compromising the supply of ES. Such a system perspective enables assessing the relationships and cascading effects in the flow of SGB to society, in turn indicating the potential impacts of hazards and their risks on both ecosystem components and services.

There are increasing approaches integrating ecological structure and ES, such as linkage diagrams (Culhane et al., 2018; Teixeira et al., 2019) or network analyses of trophic structures and ES provision (de Juan et al., 2021; Dee et al., 2017; Keyes et al., 2021; Xiao et al., 2018). The emerging interest in network approaches to understand ES provision resulted in several frameworks exploring their use in the context of ES assessment (Bohan et al., 2013; Dee et al., 2017; Marini et al., 2019; Timberlake et al., 2022; Van Kleunen et al., 2023). However, there are still efforts needed to increase the applied used of this approach to manage ES (Dee et al., 2017; Marini et al., 2019; Potschin-Young et al., 2018; Stanworth et al., 2024; The QUINTESSENCE Consortium, 2016). Network-based frameworks help elucidate interactions among ecosystem components, identify critical functional groups, and assess potential cascading effects on ES and SGB (Bohan et al., 2013; Marini et al., 2019; Timberlake et al., 2022). The high potential application of such approaches includes prioritizing protection for ecosystem functioning (Felipe-Lucia et al., 2021), linking functional diversity to multiple ES (Gray et al., 2021; Keyes et al., 2021; Windsor et al., 2023), or estimating thresholds of species loss before ES supply failure occurs (Felipe-Lucia et al., 2021; Keyes et al., 2021; Raimundo et al., 2018).

This study explores applying a network approach overview of the different steps of the ES cascade model framework, from the ecological structures and functioning to the supply of ES and associated SGB, after the input of human-capital (Elliott, 2023). The connections were then assessed between the ecological sub-system (Elliott et al., 2020) and the supply of a set of ecological functions, sustaining the supply of regulation and maintenance types of ES. These types of ES were chosen, as they are essential for sustaining ecosystem health and function, and support the supply of the other types of ES and SGB by maintaining ecological stability, resilience and resistance to human and climate-related pressures (Martínez-Harms and Balvanera, 2012; Sutherland et al., 2018). Specifically, two objectives were defined: (1) to construct a network approach representation of the ES cascade framework for the case study area, considering all the 'steps' described above; and (2) to investigate, considering the trophic structure of the ecological sub-system, the contribution of the functional groups to the supply of functions, that consequently support the provision of regulation and maintenance ES and associated SGB.

2. Materials and methods

2.1. Study area

The high-energy northern coast of Portugal (Northern East Atlantic) case study is influenced by upwelling events (Relvas et al., 2007) (Fig. 1). It features a highly urbanized coastal zone, interspersed with ecologically valuable areas along the coast and estuaries (Cunha and Magalhães, 2019). The coastal region is characterized by rocky and sandy beaches, featuring numerous reef formations with dune and back-dune formations present in some sections of the coastline. In some

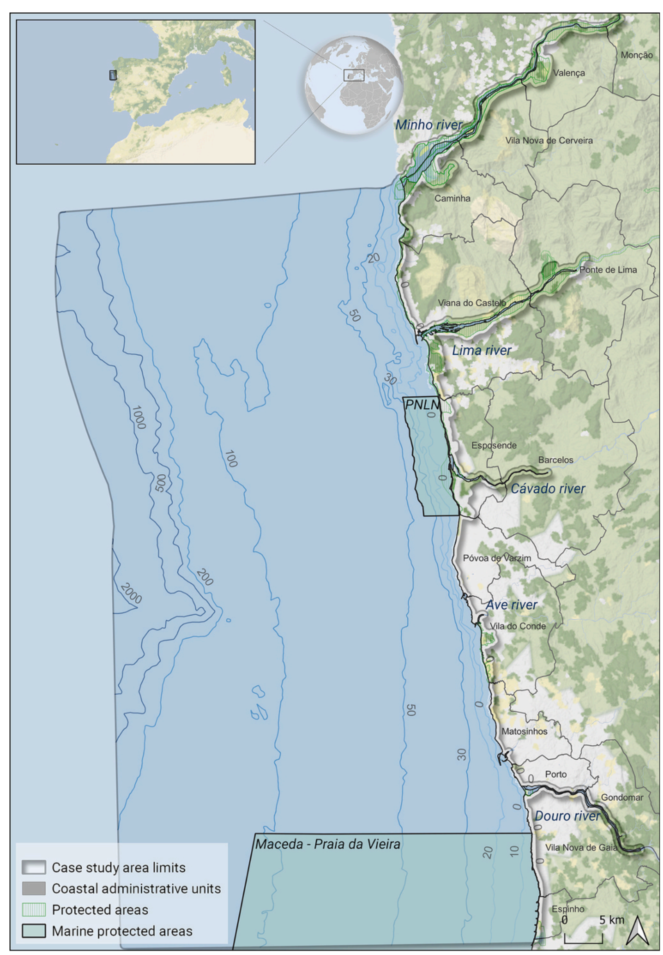

Fig. 1. Location of the case study area in the northern coast of Portugal and the current extent of protected areas and marine protected areas. PNLN – Parque Natural do Litoral Norte.

subtidal areas, the rock formations extend and contribute to the habitat of relevant kelp forests, crucial for the life cycle of many species in the region (Pinho et al., 2016). The euphotic zone extends to approximately 25 m water depth. The benthic marine system is characterized by soft bottoms with rocky substrata in certain areas. Several protected areas, protect parts of the coast and include saltmarshes in the three main estuaries providing important functions and ES such as pollutants remediation (Almeida et al., 2011, 2013), nursery, refuge and feeding grounds for fish species (Amorim et al., 2017, 2018; Ramos et al., 2010, 2017) and carbon sequestration and storage (Cunha et al., 2024). It also includes two marine protected areas, the Parque Natural do Litoral Norte, protecting important dune systems providing coastal protection against storms (Cunha et al., 2021) and 77 km^2 of important marine habitats such as macroalgae beds that provide nursery and feeding grounds (Bertocci et al., 2010; Franco et al., 2018), and the Maceda/Praia da Vieira Site, important for cetacean conservation. The region has both large scale and local fishing communities, supporting one of the largest fishing harbours of the country (Matosinhos), and industries and tourism sectors highly dependent on the regional marine natural capital. These create several pressures on the ecological structures of the region which could compromise its capacity to sustain the supply of these fundamental services. The region is impacted by high levels of coastal erosion (Antunes et al., 2019), and ocean warming, putting at risk not only coastal proprieties and the community, but also important subtidal seaweeds (de Azevedo et al., 2023), and fishing species (Szalaj et al., 2021).

2.2. ES cascade framework network overview

This section describes retrieving and processing the relevant data used to build a network overview of the different steps of the ES cascade framework for the case study area and for the regulation and maintenance ES types of ES. More precisely, this identifies the potential nodes to be represented in each network 'layer' of the ES cascade, namely: the ecological structure, composed of habitats (1) and species (2), the potential ecological functions (3) – in the case of this study, those provided only by the biotic groups – the resulting regulation and maintenance ES (4) and consequent SGB (5).

The habitat and trophic structure of the case study area was extracted from available data. A literature search, together with expert judgment, was used to evaluate the potential key ecological functions of each functional group contributing to the provision of each regulation and maintenance ES. This considers two important aspects: i) the regulation and maintenance ES are still understudied in marine and coastal realms, and ii) these types of ES constitute the fundamental contribution to the production of other classes of ES. These, also constitute the basal condition of the ecological structures and abiotic contributions to the system integrity, resistance and resilience, and the healthy system functioning provision, from which society can obtain goods and benefits (Elliott, 2023).

Following the Common International Classification of Ecosystem Services (CICES) version 5.1 (Haines-Young and Potschin, 2018), relevant classes of regulation and maintenance ES were identified for the case study region. These selected services classes were carefully evaluated and adjusted based on the case study context and modified accordingly. Attention was given to certain classes listed in CICES, where recent studies presented arguments for their classification as ecological functions rather than ES (Elliott, 2023; La Notte et al., 2017; Notte et al., 2022; Potschin-Young et al., 2017). After selecting regulation and maintenance ES classes, broader categories of SGB derived from these ES were added as an additional layer of information. The selection of functions, ES and SGB was not intended to be exhaustive but aimed to give an overview of the essential connections between ecological structure and the provision of important functions and regulation and maintenance ES and their associated SGB.

2.2.1. The ecological structure

2.2.1.1. Habitats. Seabed habitat data for the case study area were obtained from the European Marine Observation Data Network (EMODnet) Seabed Habitats project (Vasquez et al., 2021). Benthic habitats were classified into photic and aphotic habitats using a 25 m water depth threshold. Pelagic habitats, including estuarine waters and photic and aphotic marine waters, were also integrated. Coastal habitats and transitional water boundaries were extracted from the 2021 Portuguese Simplified Land Occupancy dataset (COSsim, Costa et al., 2022). Intertidal coastal habitats such as intertidal sand and rocky shores were identified using 2018 orthorectified photographs covering the entire case study area, spanning the area between the mean low water line and the mean swash line (Boak and Turner, 2005).

2.2.1.2. Functional groups. Representative functional groups across the coastal-sea continuum were identified from multiple sources. Marine data were extracted from an Ecopath mass-balance model of the Portuguese continental shelf (2006–2009), the only available trophic model for the region (Veiga-Malta et al., 2019). This model with a pedigree index of 0.54, showed a good quality of the model build data used, and incorporated 32 functional groups and their trophic interactions, that were used for the subsequent analysis (see Table S1 and Veiga-Malta et al., (2019) for further information). Biomass values were used only for visualization purposes. Groups were categorized by ecological and biological similarities and included birds, cetaceans, fish, macroinvertebrates, zooplankton, phytoplankton, and two types of detritus (detritus and fisheries discards, with the latter not being included in this work) up to a depth of 200 m. To extend coverage to the marine-coastal continuum, additional representative groups were included: Micro and Macro-algae, Macrophytes, and Terrestrial plants (Embryophyta), which contribute to important Regulation and Maintenance ES in the region (Cunha et al., 2021). The group Microorganisms was also included, although there is very little available literature information to relate this trophic group to the remaining food-web components. Trophic links between marine functional groups were extracted from the Ecopath model, and no trophic interactions were included for the intertidal and terrestrial groups, due to the lack of data, although they could occur, particularly e.g. in the herbivory of Micro and Macro-algae by other groups. Notably, some Ecopath model groups represented single species, mainly higher trophic levels, whereas others represent multiple species (Table S1).

2.2.1.3. Functions. Eleven ecosystem functions provided by the biotic components of the case study ecological structure were identified and are outlined in this section. *Primary production*, a crucial function in both the pelagic and benthic systems (Costanza et al., 2007), was separated into pelagic producers (Phytoplankton) and benthic and coastal producers (Micro- and Macro-algae Macrophytes, and Angiosperms). The coastal zone is strongly influenced by seasonal upwelling during spring and summer (Fiúza, 1983) and features rock substrata supporting kelp and macroalgae beds, and contributing significantly to the benthic primary productivity (Araújo et al., 2009; Franco et al., 2018; Pinho et al., 2016).

Filtration of Suspended Matter indicates the ability of bivalves and other filter feeders to filter organic and inorganic particles, as well as other substances from the water column. This function contributes to several regulation and maintenance ES, including water quality regulation, control of eutrophication, and the bioaccumulation of toxic substances (Vale, 2020). Within the case study area, hard and soft intertidal habitats and sea bottoms support various invertebrates, particularly bivalves, which have a significant role as filter feeders (Boaventura et al., 2002, 1999).

Microorganisms, including bacteria and other microbial organisms, constitute a widespread and highly diverse group crucial for

Biogeochemical Transformations. They play key roles in ecosystem maintenance by cycling nutrients, and degrading compounds (Arrigo, 2005).

The *Material Accumulation* function relates to the biological accumulation and incorporation of inorganic and organic materials through feeding processes such as those of burrowing organisms (e.g. resuspension and sedimentation of materials) (Dolbeth et al., 2021). It also represents the accumulation of sediments facilitated by the presence of algae and coastal terrestrial and intertidal vegetation (Salgueiro and Caçador, 2007). These groups play a vital role in consolidating and maintaining dune systems, upholding the coastal line and seabed, and accumulating nutrients and other substances.

The function *Attenuation of Wave Forces* denotes the role of biological organisms in mitigating ocean energy, particularly wave action, on seabeds and coastlines (Liquete et al., 2013; Morris et al., 2020). In the case study area, biogenic reefs, macroalgae, and kelp beds are significant in safeguarding the coastline by attenuating wave forces during storm events.

The CICES class 'Lifecycle Maintenance, Habitat, and Gene Pool Protection,' although a significant regulation and maintenance ES supporting the maintenance of various species and diverse ecosystems, is debatable regarding its classification as a "final" ES (Elliott, 2023; Hattam et al., 2015). Some studies classify it as a potential final ES (Liquete et al., 2016), while others consider it a supporting function for species lifecycles (La Notte et al., 2017) or an "intermediary service" not directly linked to human well-being (Notte et al., 2022; Potschin-Young et al., 2017). In this study, no direct links were identified to final ES or SGB directly enjoyed by society, other than supporting overall system integrity, biodiversity, and populations of various fish and commercial fish populations. Accordingly, this class was divided into four ecosystem functions supporting all species life stages and their migrations, promoting the maintenance of populations, as well as their gene pool, and preserving biodiversity. Here, the *Spawning Habitats* function, provides essential habitats for reproduction, while the *Nursery Habitats* function involves the provision of necessary habitats for the early life stages of species, promoting the continuity of viable populations (Amorim et al., 2018; Ramos et al., 2010). The *Refuge Habitats* function, provides crucial refuge areas from predators for all life stages (Bertocci et al., 2010), while the *Feeding Grounds and Species* function, relates to the provision of habitats and species for feeding, contributing to food web dynamics. These functions are exemplified in rocky and sandy bottoms, estuaries, and select coastal regions, along with associated prey populations (Amorim et al., 2018, 2017b; Ramos et al., 2015). In addition, other functions related to ecological interactions resulting from food web dynamics were incorporated into the broader category of *Ecological Interactions/Food Web Dynamics*.

2.2.1.4. Ecosystem services. Following the CICES classification system, twelve regulation and maintenance ES were identified in the case study area.

The category '*Mediation of wastes, toxics and other nuisance substances*' used two subcategories: 'Wastes and toxic substances treatment by living processes' and 'Waste and toxic substances removal and storage'. Within these classes, focus placed was solely on the potential contributions of each functional group to the treatment, deposition, and storage of anthropogenically-derived hazardous substances, such as oils, sewage residuals, heavy metals or emerging pollutants.

The '*Mediation of Smell, Noise, and Visual impacts*' entails the in-situ removal, transport, or protection against elements that might cause disturbance to society, such as the dispersal or consumption of organic wastes arriving on the coast by birds or other organisms (Culhane et al., 2018).

The '*Sediment Retention and Erosion Prevention*' involves the in-situ stabilization of sediments by vegetation and algae, crucial for maintaining the coastline in the study region, preserving existing dune systems, and preventing estuarine erosion (Coelho et al., 2009). The '*Flood protection*' ES is essential for safeguarding the coastline against wave energy and storm events and is provided by coastal habitats and species (Cunha et al., 2021). This service can be classified as a regulation and maintenance ES or a Benefit, depending whether protection targets the natural system (ES) or human infrastructure and capital (SGB) (Elliott, 2023).

The CICES groups regulating soil and water conditions were categorized into distinct regulation and maintenance ES classes, reflecting the diverse metabolic pathways involved in biotic-assisted regulation of nutrients, and the physicochemical properties, or the processing and removal of hazardous and toxic substances (Watson et al., 2016). Four main types were identified: *i) 'Biogeochemical Transformations'* by microorganisms regulating soil and water chemical conditions; (ii)'*N_2 Fixation*' by algae, macrophytes, and other intertidal and coastal vegetation (Hayes et al., 2019); (iii)'*Burying and Recycling*' of sediments and materials by macro and microbenthic organisms (Jenkins et al., 2008), and (iv)'*Incorporating substances*' through ingestion of other organisms or organic matter.

'*Climate Regulation',* encompasses the roles of the functional groups in regulating atmospheric gases, accumulating carbon, or storing it in sediments.

2.2.1.5. Societal goods and benefits. An additional layer comprising examples of ten broad SGB categories was incorporated in the network, for which human capital is required for society to derive goods and benefits from ES, either by inputting energy, time, skills, knowledge, money or the ability for humans as sentient beings (Elliott, 2023; Elliott et al., 2017). The SGB encompassed in this final layer include the provision of Clean Air, Water, and Soils, Avoided Costs, Reduction of Damages, Avoided Sediment Pollution, Ecosystem Integrity, Climate Regulation, Human Health, and Food Provision.

2.3. Connecting of the ES cascade steps

A network approach was employed to integrate the steps of the ES cascade within the case study area, with each step of the ES cascade assigned to a network layer. Each habitat, functional group, function, ES, and SGB corresponded to a node in the respective layer. Edges between nodes represent the existence of a relationship. Functional groups were connected to the habitats they occupy, and trophic relationships were based on Veiga-Malta et al., (2019), with the proportion of each group in the predator–prey relationship included as a link attribute, except in the case of the added groups mentioned above. This network 'layer' was the only one where intra-layer links were present, due to data availability. Functional nodes were connected to species performing each function based on a review of literature, with links present assigned a value of '1′. The same procedure was applied to connect functions to the regulation and maintenance ES layer, and from these to the SGB layer.

The resulting layered network encompassed six types of relationships: (1) *Habitat-Species* links (inter-layer links): representing habitats occupied by each functional group; (2) *Species-Species* link (intra-layer links): representing the trophic interactions between prey and predator; (3) *Species-Function* links (inter-layer links): representing ecological functions directly provided by each group; (4) *Function-ES* links (inter-layer links): connecting functions to ES; (5) *ES-SGB* links (inter-layer links): representing potential broad groups of SGB derived from the regulation and maintenance ES; and (6) *Function-SGB* links (inter-layer links): connecting functions directly linked to SGB, namely the functions related to the CICES class Lifecycle Maintenance, Habitat, and Gene Pool Protection. This structure provides an overview of potential pathways from the ecological structure to SGB.

2.4. Function provision support analysis

This study focussed on analysing the provision of ecological functions, underpinning the provision of regulation and maintenance ES by different trophic groups of the ecological sub-system in the natural domain (Elliott, 2023; Elliott et al., 2020), specifically by topologically analysing the sub-network '*Functional groups – Functions*', following Keyes et al., (2021). Direct function provision was evaluated using the indegree centrality, representing the number of functional groups contributing to each ecological function (and also the potential redundancy in function supply), calculated with the iGraph R package v1.4.0 (Csárdi and Nepusz, 2006). The mean trophic level of functional groups directly linked to each function was also calculated.

Beyond direct provision, function supply may receive indirect support through trophic interactions, facilitating nutrient or energy transfer (Dunne and Williams, 2009; Pocock et al., 2012; The QUINTESSENCE Consortium, 2016). To quantify these indirect contributions, a modified PageRank™ approach was applied (Dobson, 2009; Keyes et al., 2021; Wang et al., 2020). The PageRank algorithm employs a random walker in a directed network. The network direction was altered so that links pointed to ecological functions, and from consumers to prey and the random walks were initiated at function nodes. The damping factor (α) was set to 0.15. Each functional groups PageRank score represents its importance in indirectly facilitating nutrient or energy transfers to other groups (Allesina and Pascual, 2009; Bryan and Leise, 2006; Keyes et al., 2021). Functional groups directly providing a function were excluded from this analysis to avoid double-counting, since their direct contribution was already calculated as described above. Eleven PageRank values were calculated per functional group, corresponding to the eleven ecological functions, and the mean score across functions was used to rank overall group indirect contributions. Micro- and macroalgae, macrophytes, terrestrial plants, and microorganisms were excluded from this analysis due to insufficient trophic data.

3. Results

3.1. Ecological structure

Fifteen habitats were defined: coastal dunes and sandy shores (13.23 km^2), saltmarshes (8.53 km^2), intertidal littoral rock and biogenic reefs (4.16 km^2), intertidal littoral sediment (2.03 km^2), estuaries – pelagic (37.21 km^2), estuaries – bottom (37.21 km^2), photic pelagic waters (344.34 km^2), aphotic pelagic waters (4496.21 km^2), photic rock and biogenic reef (109.29 km^2), photic sand (215.34 km^2), photic mud (19.72 km^2), aphotic rock and biogenic reef (1228.47 km^2), aphotic mixed sediment (479.83 km^2), aphotic sand (892.53 km^2), and aphotic mud (1895.38 km^2) (Fig. S1). The pelagic realm, including both aphotic and photic zones, covered most of the study area. Circalittoral mud benthic habitats represented the predominant benthic sea area, while photic hard bottoms covered an area of approx. 110 km^2. Model derived trophic data showed Meso- and Microzooplankton, Phytoplankton, Sardines, Macrozoobenthos and Benthopelagic invertivorous fish, as the

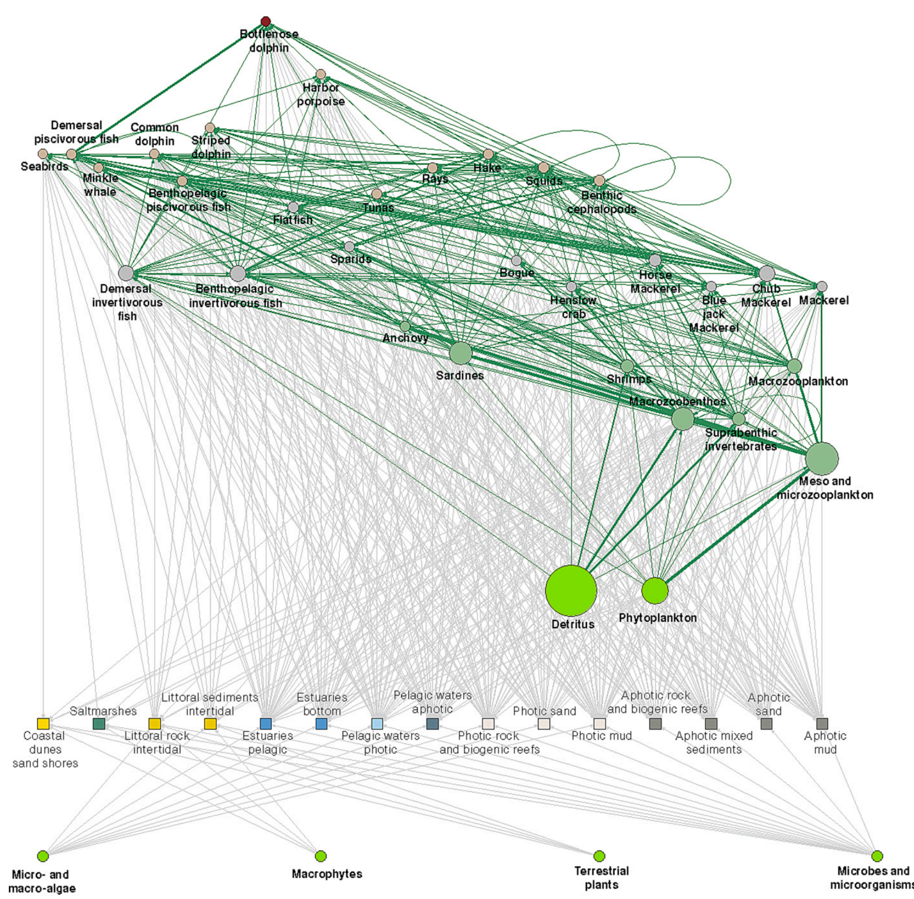

Fig. 2. The established connections between the functional groups and the potential habitats (Habitat-Species sub-network) inhabited by each one (grey lines). The size of the nodes representing the functional groups corresponds to their relative biomass (log scaled) in the trophic model of Veiga-Malta et al., (2019), except for the groups Micro and Macro-algae, Macrophytes, Terrestrial plants and Microbes-Microorganisms (as no data were available). Green lines show trophic interactions between biological groups. The thickness of the green lines represents the proportion of prey in the predator's diet. The size of nodes in the food web corresponds to the biomass of the group in the trophic model. The colours of the food web nodes, from bright green to dark brown corresponds to their trophic level extracted from the model, from 1 (bright green) to 5.3 (dark brown).

functional groups with the highest biomass in the case study area (Table S1). The ecological structure of the study area was characterized by the connections between the functional groups and the habitats they occupied (Fig. 2, Table S2), thereby establishing the potential service providing units within the case study area.

3.2. Ecosystem cascade network overview

The multi-layered integration of the various steps in the ES cascade shows the intricate connections among the habitats, functional groups, functions, regulation and maintenance ES, and subsequent SGB (Fig. 3 shows the full overview, Fig. 2, Fig. 4a and 4b, the various sub-networks, Tables S2-S6 show the links between nodes).

The overall multi-layered network, highlights the multifunctionality of the case study region, both in terms of ecological function and of ES and consequent SGB supply. On one hand, the complexity of the ecological structure supports the supply of multiple ecological functions, with many functions contributing simultaneously to several ES (e.g. Waste and toxic substances treatment or removal or Water quality regulation). On the other hand, multiple ES and functions contributed to each SGB, especially in relation to Clean Water, Soils or Water or the Maintenance of Ecosystem Integrity. Notably, most SGB were supported by multiple ES, with only two exceptions, Human Health, derived solely from Pest and Disease Control, and Climate Regulation, provided exclusively by Global, Regional, and Microclimate Regulation through carbon sequestration and storage.

3.3. Ecological function provision analysis

After constructing the full network, the analysis was focused on the '*Functional group–Function*' sub-network (Fig. 4a) and gave two main patterns. Firstly, some ecological functions and their associated ES were supplied exclusively by a single functional group (Table 1). For instance, Pelagic Primary Productivity was dependent solely on phytoplankton, and Microbial Activity was inherently linked to microbes and microorganisms. In contrast, 'Material Accumulation' and 'Ecological Interactions/Food-web dynamics' were ubiquitous across all groups in the food-web (Table 1, Table S8), whereas most other remaining functions were provided by relatively few groups. Secondly, most regulating and maintenance ES were supported by multiple ecological functions, with the exception of 'Flood protection', provided only through attenuation of wave energy. Similarly, Pest and Disease Control resulted from the emergent qualities and maintenance of trophic interactions among various functional groups.

Direct contributors to function supply were mainly the lower trophic levels groups, namely the groups algae and macroalgae, macrophytes, macrozoobenthos, suprabenthic invertebrates and terrestrial plants (Fig. 5). Phytoplankton, zooplanktonic groups, crabs and shrimps also supplied a higher number of functions.

In addition to the direct contribution to the supply of ecological functions, the biotic functional groups could also indirectly contribute or hinder function and the potential ES supply through their trophic interactions. The indirect contributions, assessed through the trophic interactions analysis, revealed the planktonic groups as key indirect supporters of other groups directly supplying the functions (Fig. 6, Table 1, Tables S7 and S8). Phytoplankton and zooplankton were the greatest contributors, with values higher than the overall mean contribution across the entire food-web. Indirect support generally declined with increasing trophic level, highlighting the central role of lower-trophic groups in sustaining regulation and maintenance ES provision.

4. Discussion

Understanding the regional-to-local pathways of ES provision, from ecological structure and functioning to ES and SGB, is important to implementing an ecosystem-based management approach in marine and coastal systems. This study adopted a conceptual approach based on the ES cascade framework (Haines-Young and Potschin, 2018, 2010),

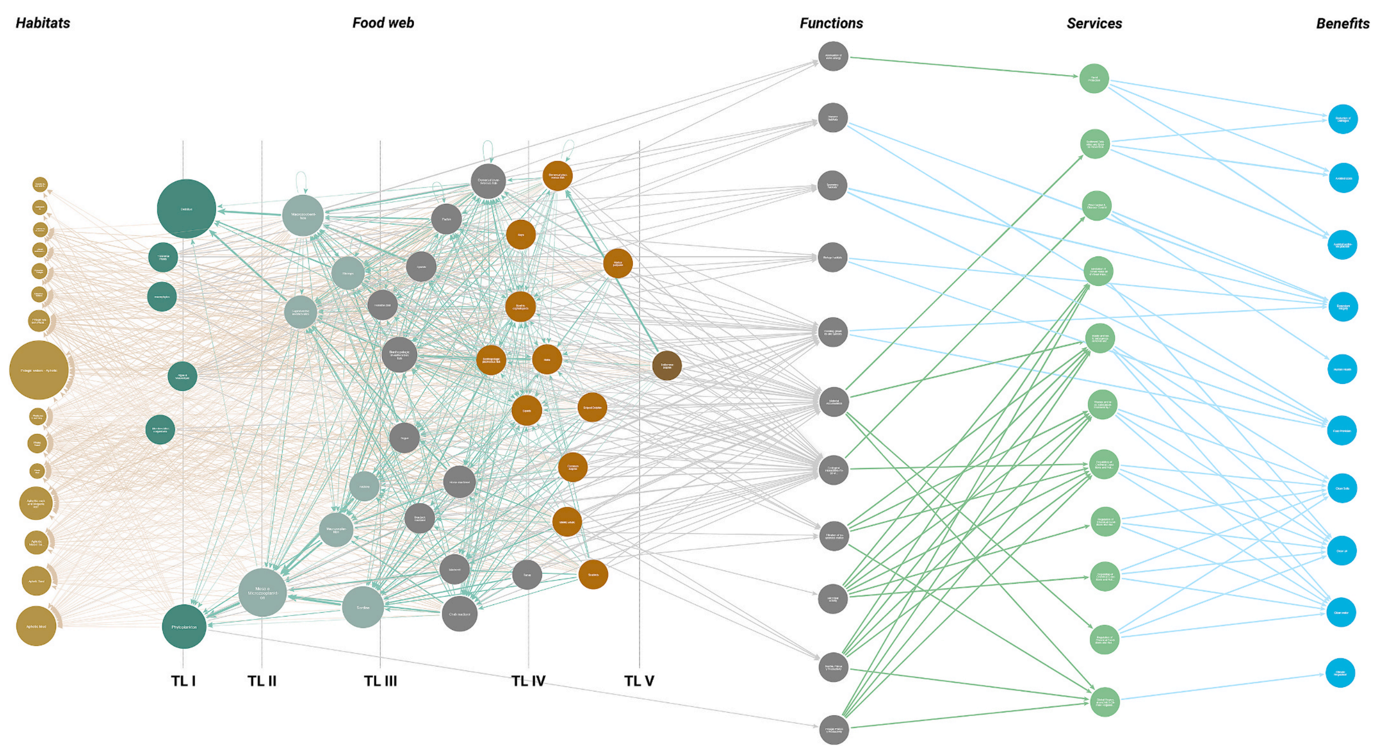

Fig. 3. The representation of the full ecosystem services cascade framework network overview in the case study area, from the ecological structure composed of the habitats and functional groups layers, to examples of functions they provide and subsequent ecosystem services and obtained societal goods and benefits. The size of the nodes representing the habitats are their relative area. The size of nodes in the food web corresponds to the biomass of the group in the trophic model. TL – Trophic level.

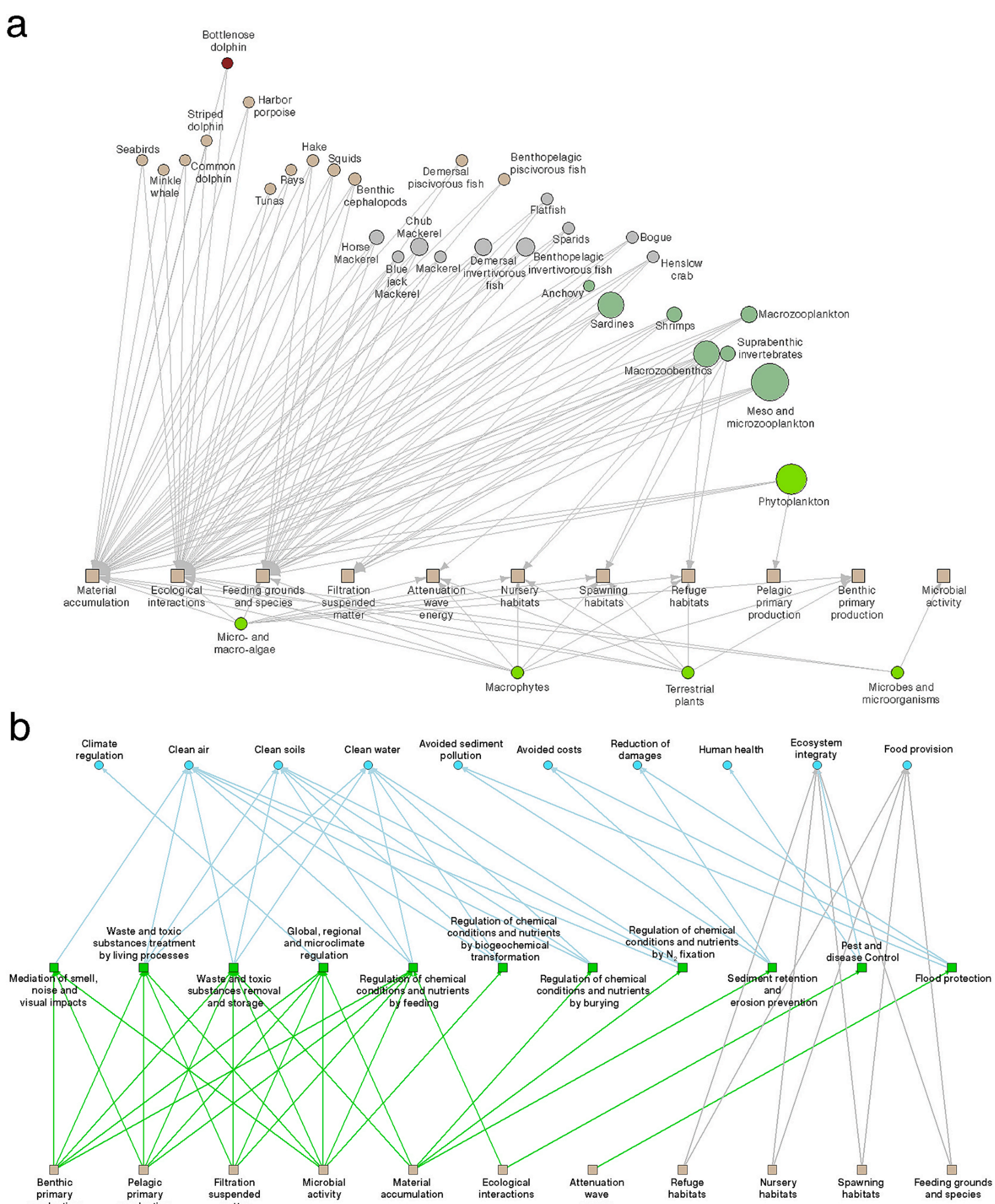

Fig. 4. Overview of the various network layers of the steps of the ecosystem services cascade framework within the study area from Fig. 3. The sub-network *Functional groups – Functions* (a), and the *Functions – ES, ES – Societal Goods and Benefits* and the *Function – Societal Goods and Benefits* sub-networks (b). (a) Grey lines illustrate the provision of each function by each biotic group ('*Functional groups-Functions*' sub-network). Size of the circle in the food web corresponds to the biomass of the group in the trophic model. (b) Links between functions (brown squares) provided by the biotic groups, the regulation and maintenance ecosystem services considered in this study (green squares) and potential Societal Goods and Benefits (blue circles). Light green lines indicate the links between ecological functions and ecosystem services. Light blue lines show the links between ecosystem services and Societal Goods and Benefits. Grey lines indicate the links between ecological functions and Societal Goods and Benefits.

through a network approach, integrating food-web and ecological function analysis to trace direct and indirect pathways of function and ES provision. This study represents, to our knowledge, the first application of the ES cascade through a network perspective, thereby creating opportunities for future adaptations and refinements of the approach.

The focus was on ecological functions and the regulation and maintenance ES types of ES, which underpin the supply of the other ES, sustain system resistance and resilience to change, and support good ecological and environmental status (Millennium Ecosystem Assessment, 2005). These also provide the foundation for obtaining SGB after inputting human and complementary capital and assets (Elliott, 2023). Although this analysis addressed the ecological functions and regulation and maintenance ES supply, the approach can be extended to additional functions and types of ES and SGB.

The low to mid-trophic level groups are crucial contributors to the supply of the ecological functions and regulation and maintenance ES under study, both directly through their functional roles and indirectly by interactions, such as serving as prey for groups directly contributing to function supply. The planktonic groups, both phytoplankton and zooplankton, stand out as the main indirect contributors to functions and consequently regulation and maintenance ES supply. This finding is especially relevant in this upwelling system and aligns with patterns

Table 1
The mean trophic level of the functional groups providing each function, the number of functional groups directly supplying the ecological function, and the number of groups contributing to the provision of each ecological function, across the case study area.

Ecological function	Mean trophic level	Groups directly providing the function	Groups supporting the function provision
Pelagic Primary Productivity	1	1	0
Benthic Primary Productivity	1	3	0
Filtration of suspended matter	2.5	6	18
Microbial activity	1	1	0
Material Accumulation	3.2	35	35
Attenuation of wave energy	1	3	0
Nursery habitats	1.5	5	5
Spawning habitats	1.5	5	5
Refuge habitats	1.5	5	5
Feeding grounds and species	2.8	23	3
Ecological Interactions/Food-web dynamics	3.2	35	0

observed in similar systems (Cardinale et al., 2012; Torres et al., 2013). Consistent with other studies (Culhane et al., 2018; Ito et al., 2019; Jacob et al., 2015; Teixeira et al., 2019), these findings highlight the system multifunctionality, where multiple groups and functions jointly sustain ES supply. Such biodiversity-driven facilitation of ES supply (Balvanera et al., 2016; Cardinale et al., 2012; Jacob et al., 2015; Le Provost et al., 2023), provides spare capacity that enhances system resistance; i.e. when multiple groups support the supply of a specific function, the system becomes more robust and resilient to natural or human-induced changes. This feature has been termed environmental homeostasis which appears common in functionally variable and diverse ecosystems (Elliott and Quintino, 2007).

However, some of key regulation and maintenance ES and SGB, such as flood protection (Cunha et al., 2021) or the provision of habitats for commercially exploited species highly valued by society in this coastal-marine continuum (Amorim et al., 2018; Ramos et al., 2009), rely on a limited number of groups directly contributing to their supply. This potentially exclusive supply increases vulnerability to disturbance, as pressures affecting the fitness or trophic role of a single group may cascade to others, potentially reducing ES supply, triggering regime shifts, potential declines in supporting species, or favouring nuisance and invasive species (David et al., 2017; Dunne et al., 2013; Keyes et al., 2021; Lafferty and Kuris, 2009; The QUINTESSENCE Consortium, 2016; Xiao et al., 2018). While ES simultaneously provided by multiple groups (Dunne and Williams, 2009) or by lower trophic levels (Dobson, 2009; Jacob et al., 2015) may exhibit higher resistance and resilience, substantial knowledge gaps remain about how pressures propagate across systems (Elliott et al., 2017; Elliott and O'Higgins, 2020; Gissi et al., 2017), especially in coastal areas where land-sea interactions intensify complexity (Elliott, 2011; Van der Biest et al., 2019). While some studies have explored the consequences of species loss and its consequences on ES supply and human well-being (Ansley et al., 2023; Cardinale et al., 2012; Ross et al., 2021), approaches such as those here can help evaluate system-wide pressure impacts and their repercussions and support informed management decisions. This complexity generates uncertainty in assessment and management, particularly in the face of future threats from exogenic, unmanageable pressures such as climate change (Elliott, 2011; Halpern and Fujita, 2013). These findings reinforce the need for a holistic ecosystem-based management and integrative perspective (Bodin et al., 2019; Elliott and O'Higgins, 2020; Ostrom, 2009), where managers adopt bottom-up and integrative approaches that safeguard key ecological structures, processes and functions, to maintain the flow of SGB on which society relies (Notte et al., 2022; Smith et al., 2025).

While this study has yielded valuable insights, by applying a network approach to the ES Cascade to trace functional pathways leading to regulation and maintenance ES, it is essential to note that it did not aimed to represent the full range of ecological functions or ES outputs. Future studies should refine and expand this approach to better capture how the system supports additional functions and services, which could yield further insights. Furthermore, the food-web model aggregated

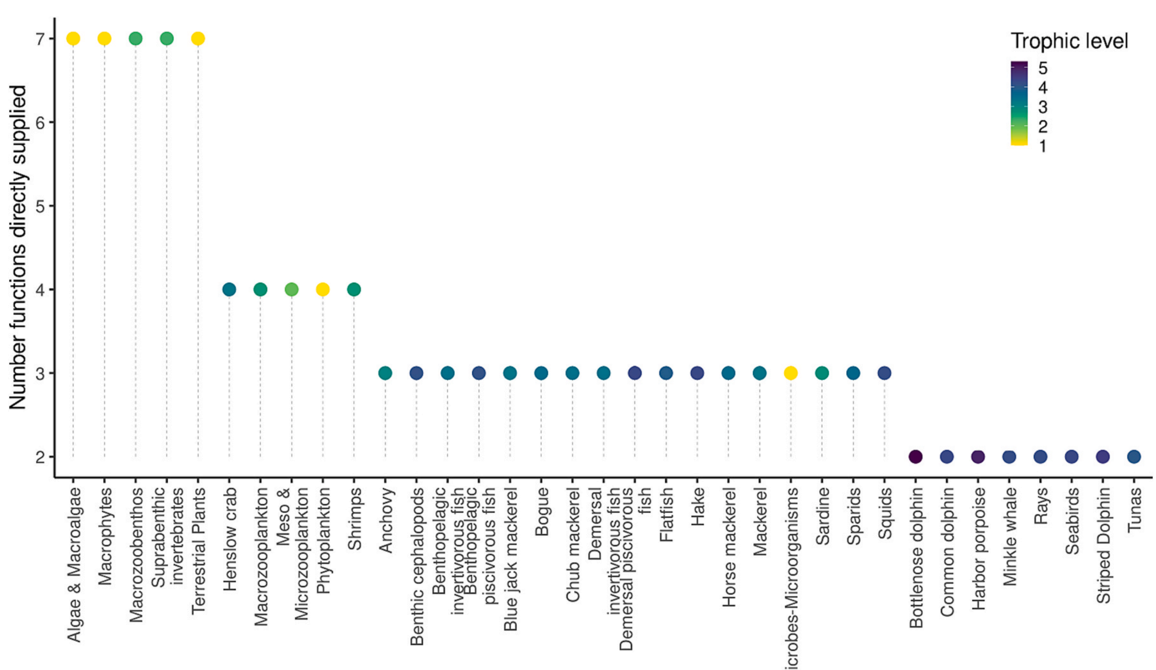

Fig. 5. Number of direct supplied ecological functions for each functional group considered in this study. Colour indicates the trophic level of the respective functional group.

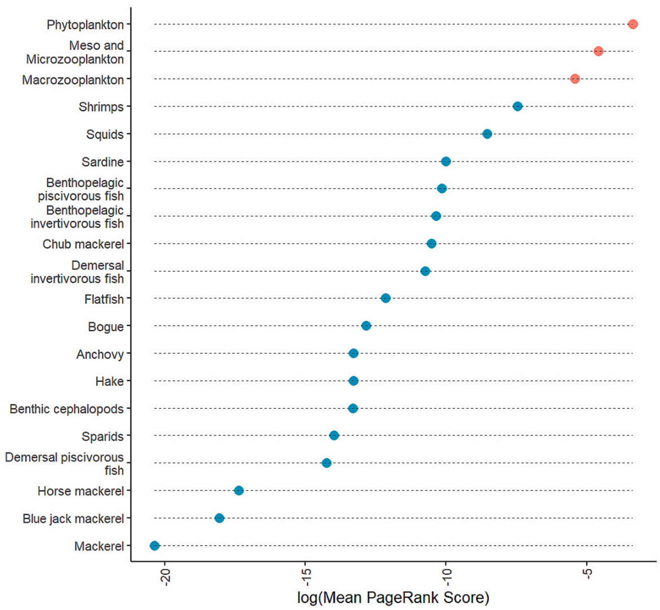

Fig. 6. The mean log values of PageRank scores for each biotic group indirectly contributing to providing the ecological functions considered in this study. Red dots identify the groups with PageRank values above the mean PageRank values. The mean PageRank values have been included in the log format for the purposes of visualisation.

species into some of the functional groups which may have influenced the results, particularly the lower trophic groups (Veiga-Malta et al., 2019). Future research could disaggregate groups into individual species (although highly complex), and include other types of ES and SGB, hitherto outside the scope of this study, such as food provisioning (e.g. fisheries), or mental and physical human wellbeing (e.g. enjoying/ watching nature, nature sports practice). In addition, while this study focused on the role of biotic components in function supply, many ES also depend on the abiotic component, which should not be disregarded, such as the existence of rock or soft bottoms for spawning, as in the case of some fish species. In addition, further layers of information could be added. Integrating potential pressures using frameworks such as the DAPSI(W)R(M) framework (Elliott et al., 2017; Elliott and O'Higgins, 2020), could help assess cascading effects and feedbacks (both positive or negative) and emphasize the importance of the social-ecological system (Smith et al., 2025). Creating methods for quantifying these links, although complex, could then greatly improve ES and SGB assessment and valuation. Moreover, incorporating a spatial information layer on habitat connectivity and species ecological niches in such a system analysis, could further refine the spatial application of these concepts (Gonzalez et al., 2017; Sayles and Baggio, 2017). These improvements would enhance the biophysical realism in ES modelling but could also better integrate the relevant socio-environmental parameters and trade-offs in their supply (Richards and Lavorel, 2023). Ultimately, understanding the potential resolution of the pathways leading to ES and SGB within a management system, through approaches as in this study, can reveal valuable previously unseen insights for decision-makers and managers (Dee et al., 2017; Elliott et al., 2020; Felipe-Lucia et al., 2021; Firkowski et al., 2021).

5. Conclusions

The application of ecosystem-based management in marine systems faces challenges due to knowledge gaps in the ecological aspects that underlie ES provision, while managers often do not fully appreciate the concepts and significance of the ecological system within the ES concepts. This study employed a theoretical network approach, integrating models, literature, and empirical data to create a network overview of the ES cascade and assess pathways of ecological function and ES supply. The resulting framework can aid managers and planners in making informed decisions about the complex ecological structure that supports ecological functions, ES supply, and the flow of SGB into society, within a management zone.

Results highlighted the importance of the lower trophic levels in directly supporting the provision of functions and consequently of regulation and maintenance ES, while planktonic groups were highlighted as key indirect support to the system ecological functioning. Some ecological functions and ES were supplied by a low number of functional groups, indicating potential vulnerability and the need for targeted conservation measures to maintain function and ES provision under environmental change and increasing anthropogenic pressures. Conversely, the redundancy of other functions and ES, supported by multiples groups, demonstrates increased potential resistence and resilience against change.

This study reinforces the importance of holistic system management, emphasizing the interconnectedness of the ecological components and the need for interdisciplinary approaches for effective management of complex social-ecological systems and the maintenance of a sustainable flow of SGB on which society relies. The conceptual approach of this study facilitates a clearer visualization of the ES cascade model within the ecological system of the case study area. This provides an understanding of the direct ecological contributors for essential ecological functions and regulation and maintenance ES supply, but also reveals its potential indirect contributors, important in sustaining the robustness and resilience of the systems trophic structure. By identifying key groups, in this case study those at lower trophic levels that serve as sole providers of specific regulation and maintenance ES, allows managers to prioritize critical components that support service provision and maintain good ecological and environmental status. In particular, this finding includes those ES and SGB most valued by society within each management zone.

CRediT authorship contribution statement

Jacinto Cunha: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Edna Cabecinha:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Funding acquisition. **Sebastian Villasante:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Funding acquisition. **Stefano Balbi:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Funding acquisition. **Michael Elliott:** Writing – review & editing, Visualization, Validation, Supervision. **Sandra Ramos:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114218.

Data availability

Data will be made available on request.

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