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Review

Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus

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ABSTRACT

The global trend in losing biodiversity is affecting ecosystems due to changes in their functions and services. Biodiversity and Ecosystem Functioning has become increasingly topical over the last decades, and still a developing research field. Marine macrobenthic fauna are important providers of ecosystem functioning by regulating the fluxes of energy and matter. However, anthropogenic impacts have triggered changes in their structure and function at the community and ecosystem level. Despite advances in recent years, a wider application of biodiversity and ecosystem functioning relationship in benthic communities has been restrained by missing information on biological traits of species and inconsistencies in terminology, methodologies and approaches used. This review synthesizes the current status of knowledge on the functional approaches of marine macrobenthic fauna and their contribution to ecosystem functioning, using a new method named research weaving analysis. We thus provide a research synthesis combining bibliometric analysis and systematic mapping (spread of evidence). We described advancements in the current knowledge and synthesized the most common functional approaches, terminology and numerical methodologies used. A conceptual step-by-step guide is presented to assist future assessments of ecosystem functioning for marine macrobenthic fauna, and suggestions made for coherent use of terminology, trait selection and metrics to measure ecosystem functioning. The analyses presented will support the development of a framework to conduct globally comparable analyses of ecosystem functioning in marine benthic ecosystems.

1. Introduction

Biodiversity is declining worldwide causing changes in ecosystem functioning and services (Sala and Knowlton, 2006; Wright et al., 2006; Butchart et al., 2010; McCauley et al., 2015; IPBES, 2019). Over the last few decades, the rate of biodiversity loss and changes in ecosystems have motivated research towards understanding the relationship between Biodiversity and Ecosystem Functioning (BEF). Research directions have included investigations on ecological processes and how changes in biodiversity affect ecosystem functioning and services, elucidating the mechanisms that underpin the biodiversity and functional relationship (Naeem et al., 2002; Hooper et al., 2005; Reiss et al., 2009; Cadotte et al., 2011; van der Plas, 2019).

Ecosystem functioning is defined as the combined effects of all natural processes that sustain an ecosystem (Table 1). The concept of Biodiversity and Ecosystem Functioning emerged in the early 1990's (Naeem et al., 1994; Tilman et al., 1996), and has evolved since then, but mainly in terrestrial (Díaz and Cabido, 2001; Tilman et al., 2014; van der Plas, 2019) and freshwater ecology (Lecerf and Richardson, 2010; Schmera et al., 2017). A large body of research shows that greater diversity leads to an increase in the number of expressed biological traits and greater effects on ecosystem functioning, compared to less diverse assemblages that have poor functional expression (Chapin et al., 2000; Hooper et al., 2005; Hillebrand and Matthiessen, 2009; Reiss et al., 2009; Snelgrove et al., 2014). The strength and direction of the BEF relationship can, however, be highly variable and subject to environmental context (Strong et al., 2015; Thrush et al. 2017; van der Plas 2019).

In order to assess the BEF relationship several approaches have been used. Functional diversity (FD) is the most relevant measure for understanding the relationship between biological diversity, the functioning of organisms, and the links to ecosystem functioning (Díaz and Cabido, 2001; Hooper et al., 2005; Wright et al. 2006; Lefcheck and Duffy, 2015; Legras et al., 2018). Functional diversity is defined as the value and range of functional traits (Table 1) and has been quantified by grouping species with shared taxonomic, physiological and

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Table 1
Terminology used in the context of Biodiversity-Ecosystem Functioning and suggested definitions for (a) general terms and (b) trait specific terms.

Key terms	Definition
(a) General terms	
Biodiversity	The extent of all genetic, taxonomic and ecological diversity over all spatial and temporal scales (Reiss et al., 2009; Snelgrove et al., 2014)
Ecosystem functioning	The combined effects of all natural processes that sustain an ecosystem (Reiss et al., 2009; Degen et al., 2018; Gladstone-Gallagher et al., 2019)
Ecosystem goods and services	The ecosystem services are the conditions and processes through which natural ecosystems sustain and fulfil human life. The ecosystems goods are products obtained from ecosystems. In general, both are products of ecosystem functioning that are of value to humans, or with benefits that humans obtain from ecosystems (Reiss et al., 2009; Snelgrove et al., 2014; Degen et al., 2018)
Ecosystem process	Changes in energy and matter over time and space through biological activity, within the ecosystem, due to abiotic (physical and chemical) and biotic (organism) factors and interactions (Reiss et al., 2009)
Ecosystem modelling	The development and analysis of mathematical and statistical models of ecological processes (Pittroff and Pedersen 2005)
Functional divergence	Degree to which the maximum abundance of functional traits deviate from the centre of the functional space within the same community (Mason et al., 2005; Mouchet et al., 2010; Schmera et al., 2017)
Functional diversity	The value and range of functional traits that influence ecosystem functioning (Tilman et al., 1996; Díaz and Cabido, 2001; Reiss et al., 2009; Schmera et al., 2017; Degen et al., 2018)
Functional evenness	Distribution of abundance among functional traits (Mason et al., 2005; Mouchet et al., 2010; Schmera et al., 2017)
Functional richness	Amount of functional trait space occupied by an assemblage of multiple species (Mason et al., 2005; Mouchet et al., 2010; Schmera et al., 2017)
(b) Trait terminology	
Trait	Any morphological, physiological or phenological feature measurable at species level.
Biological trait	A defined and measurable (presence/absence, or fuzzy coding) property of organisms, usually at the individual level and used comparatively across species (Reiss et al., 2009; Degen et al., 2018)
Functional trait	Component of an organisms' phenotype that determines its effect on ecosystem functioning; also referred to as functional characters (Petchey and Gaston, 2006; Reiss et al., 2009; Degen et al., 2018; Weiss and Ray, 2019)
Effect traits	Expression of a trait that shapes how organisms affect ecosystem functioning (Beauchard et al., 2017; Degen et al., 2018)
Response traits	Traits that determine how organisms respond to changes in the environment (Degen et al., 2018)
Trait modalities	Categories in which any trait can be subdivided

morphological characteristics (Wright et al., 2006). The number of ways to measure FD is continually evolving, but usually split into three main components; (1) functional richness, (2) functional evenness, and (3) functional divergence (Petchey and Gaston, 2006; Mouchet et al., 2010; Legras et al., 2018, see Table 1 for definitions). However, numerous other metrics to measure FD have been developed over time (e.g. community bio-irrigation potential, community weight means, functional complementary, functional redundancy, functional regularity and Rao's Quadratic Entropy) (Petchey and Gaston, 2006; Cadotte et al., 2011; Queiros et al., 2013; Song et al., 2014; Schmera et al., 2017).

Functional diversity generally involves knowledge of the components of biodiversity that influence ecological processes or ecosystem functioning (Petchey and Gaston, 2006; Schmera et al., 2017), whereby approaches that measure FD are usually based on functional traits (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Hillebrand and Matthiessen, 2009). Functional traits are the components of an organisms' phenotype that determine its effect on ecosystem functioning (Petchey and Gaston 2006; Reiss et al., 2009; Degen et al., 2018; Weiss and Ray 2019). Functional traits can be selected by either (1) incorporating a wide range of information on biological traits regardless of the taxonomic group (Cadotte et al., 2011; Verissimo et al., 2012) or, (2) selection of an appropriate set of traits that depend on the specific objectives and processes to be measured in any particular study (Reiss et al., 2009).

Marine macrobenthic communities in soft sediments are important providers of ecosystem functioning. They regulate the fluxes of energy and matter and are bioindicators of ecosystem health due to their sensitivity to natural and anthropogenic disturbance (Borja et al., 2000; Reiss et al., 2009; Snelgrove et al., 2014; de Juan et al., 2015; Lefcheck and Duffy, 2015). Anthropogenic disturbances such as trawling, dredging or pollution, can affect growth, mortality, recruitment rate and dispersal ability of benthic species (Lohrer et al., 2010, Naeem et al., 2012; Villnäs et al., 2013; Dannheim et al., 2014; Shojaei et al., 2015), altering the structure and functioning of benthic communities (Worm et al., 2006; van der Linden et al., 2012; Thrush et al. 2017), and therefore ecosystems.

Efforts have been made to understand, describe and measure BEF relationships for macrobenthic fauna in marine ecosystems, using manipulative experiments (Stachowicz et al., 2007), analysing the seafloor biodiversity-ecosystem functioning (Snelgrove et al., 2014), creating frameworks for polar oceans (Degen et al., 2018), and describing the functioning of mudflats (Dissanayake et al., 2018). However, several gaps persist in the knowledge of ecosystem functioning in benthic communities, arising from missing information on the biological traits of specific species, and inconsistency in terminology, methodologies and approaches used (Tyler et al., 2012; Strong et al., 2015; Thrush et al., 2017; Paterson et al., 2019). A framework describing the links between macrobenthic fauna, biological traits, ecological processes and ecosystem functioning and services is thus still missing.

In order to advance a more coherent approach in BEF of marine macrobenthic fauna, we present a research weaving analysis, combining bibliometric analysis with systematic mapping (Nakagawa et al., 2019). This novel approach allowed an advanced and visualised synthesis of the research to date about the connection between biological traits, ecological processes, and ecosystem functions. Through the systematic review of BEF literature on marine macrobenthic fauna around the world, we provide an overview on the spread of evidence and bibliographic analysis. We further analysed the literature content under several categories to identify how ecosystem functioning and functional diversity are currently conceptualized and measured. To enhance comparability between studies, we encourage the use of a general and standardized approach that includes coherent terminology, quantitative methods for choosing biological traits, and consistent use of metrics to measure ecosystem functioning. We also provided a conceptual step-by-step guide to assess ecosystem functioning for marine macrobenthic fauna.

2. Methods

2.1. Literature and database mining

The databases SCOPUS (Elsevier; elsevier.com) and Web of Science (WoS, Thompson Reuters; webofknowledge.com) were used to compile all studies published before November 2019. The literature searches were performed using the tool 'combination of sets' (WoS) and 'combine queries' (SCOPUS), which allowed us to find the articles that contained any of all the possible combinations using the following terms: 'macrofauna', 'macroinvertebrate(s)', 'macrobenthic', 'ecosystem function(ing)', 'ecosystem multifunctionality', 'functional diversity',

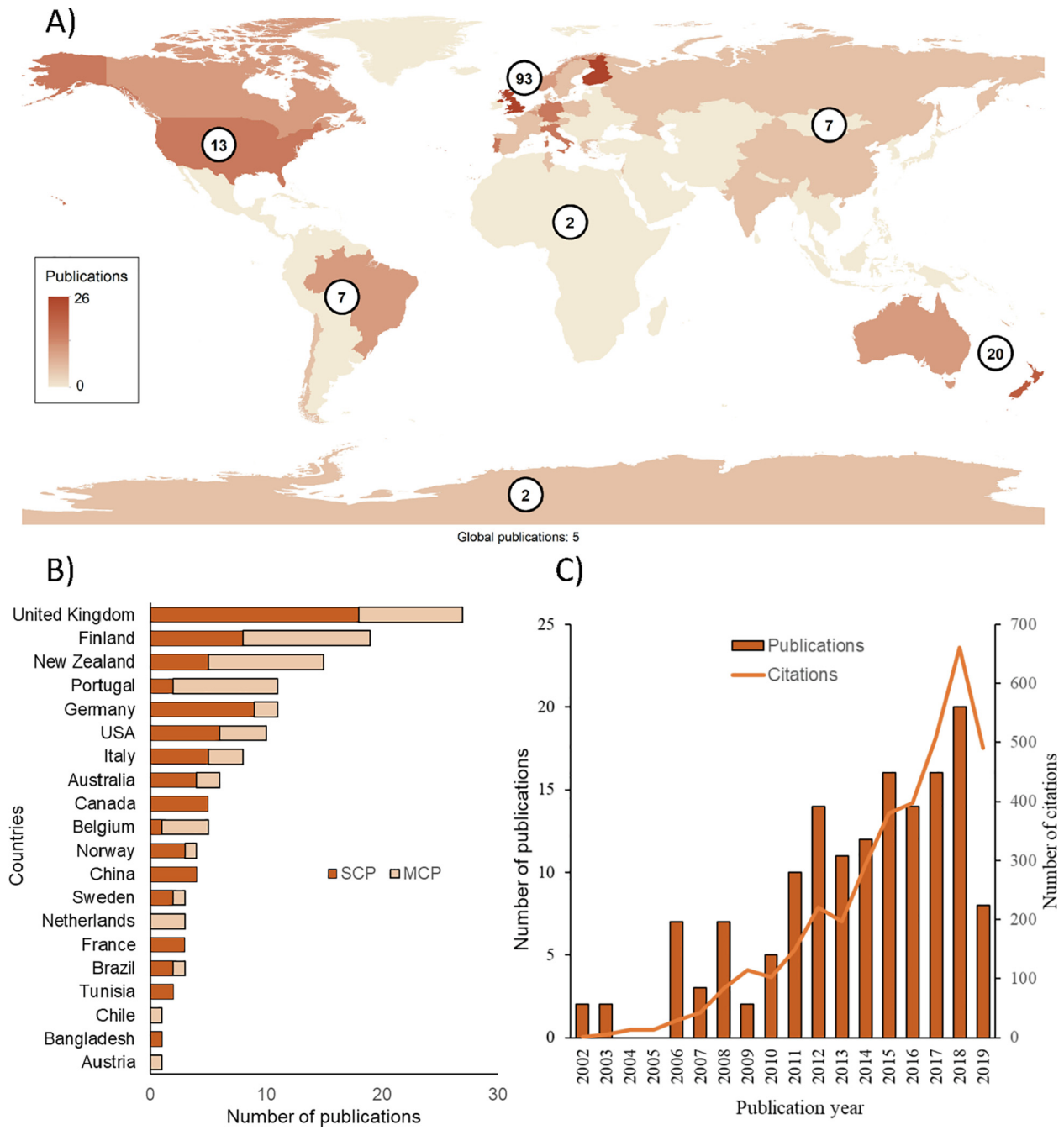


Fig. 1. Spread of evidence of studies on ecosystem functioning of marine macrobenthic fauna. A) Geographical distribution of the origin of the publication of the included studies. Numbers inside of circles represent the number of publications per continent. Colour intensity is proportional to the number of first authors affiliated to a given country. B) The top 20 most productive countries; SCP: single country publication; MCP: multiple country publication. C) The number of peer-reviewed publications and citations on ecosystem functioning of marine macrobenthic fauna across time.

'functional traits', 'biological traits'; in the fields of 'Article title, Abstract, Keywords' for SCOPUS and; in 'topics' (Article title, Abstract, Author, Keywords and Keywords plus) for WoS. This search resulted in 1813 published studies (1092 in SCOPUS, all of them were in WoS). Within these results, a primary examination of the titles and abstracts was done, retaining only the publications that met the following criteria of: (1) environment (marine habitat), (2) organisms (all macrobenthic fauna), (3) statistically tested, and (4) study type (e.g. only scientific peer-reviewed publications), yielding a total of 239 publications. A second and final examination of the publications was done where we carefully read through each article to verify its relevance to ecosystem functioning of marine macrobenthic fauna, resulting in 93 publications that did not meet the required criteria. In addition, a cross-referencing of the publications gathered additional publications outside of the initial review process (3 publications), resulting in a final total of 149 publications on the research field of ecosystem functioning and functional diversity of marine macrobenthic fauna that included soft and hard bottom marine habitats (Table S1 in supplementary material).

2.2. Review style and data analyses

To investigate the relationship of marine macrobenthic biodiversity and ecosystem functioning, we performed a new systematic approach named 'research weaving'. This type of research synthesis combines

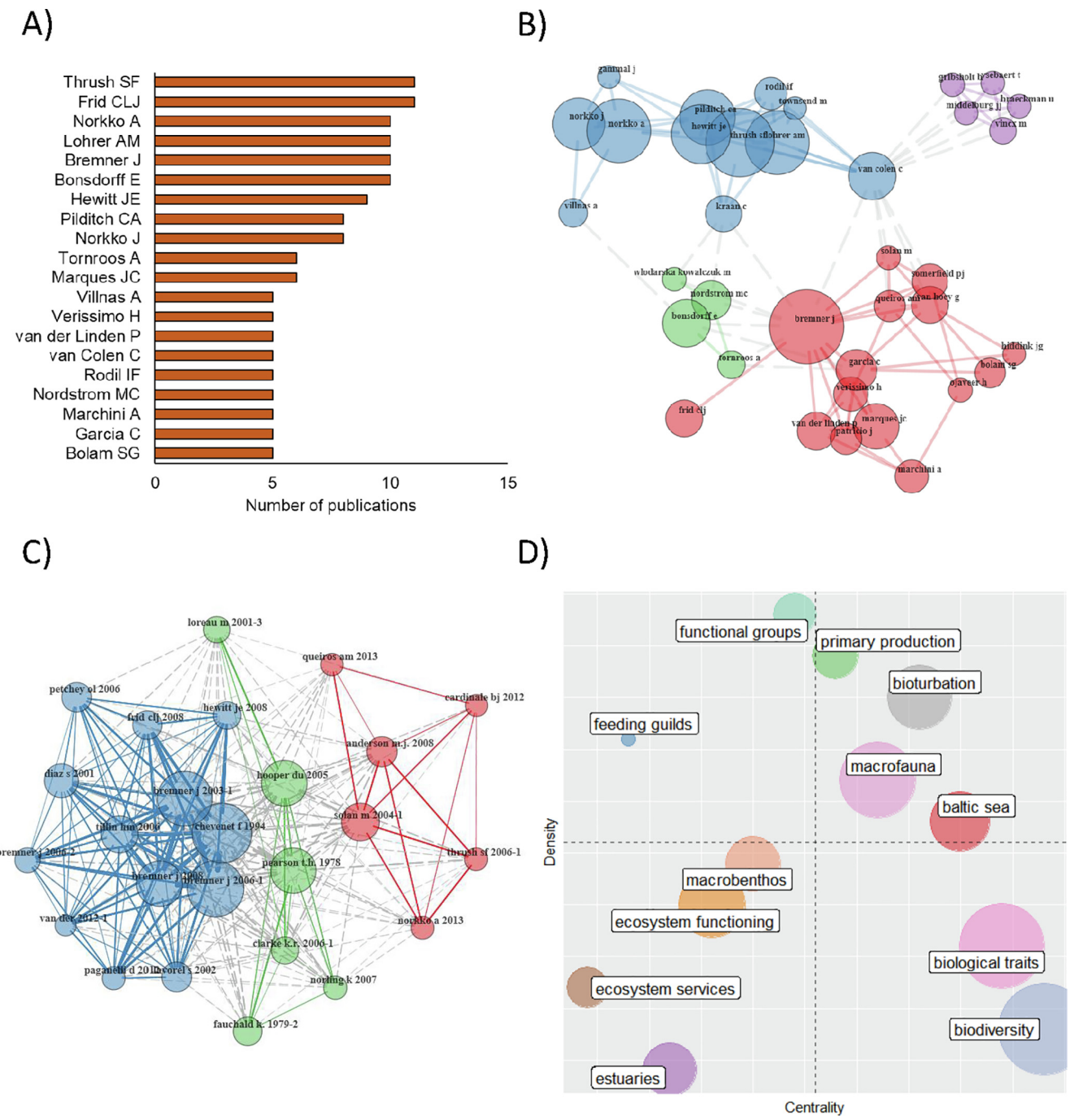


Fig. 2. Bibliographic analysis of publications on ecosystem functioning of marine macrobenthic fauna. A) Most productive authors. B) Author collaboration network. Nodes represent relations between the top 35 authors in terms of the numbers of authored publications in the dataset; line connections are co-authorships; nodes size is proportional to the number of publications; node colours represented strongest associations between networks. C) Co-citation network based on publication references. Nodes represent relations between cited publications using the top 20 most cited authors; node size is proportional to the number of times the article was cited; nodes colours represented strongest associations between networks. D) Thematic map of keywords based on co-word analysis through authors keyword co-occurrences.

bibliometrics and systematic mapping, summarizing and visualizing the information content, history and networks across and within publications of a specific topic (Nakagawa et al., 2019).

Bibliographic analyses were performed using the bibliometrix-R package (Aria and Cuccurullo, 2017) in R v3.5.0 (R development Core Team, 2018). An author collaboration network was created using a 'fruchterman' method base on the top 35 authors with more collaborations. For the co-citation network, we used the 25 most co-cited publications and a 'fruchterman' method. The thematic map of keywords was performed using a co-word analysis based on the authors key words.

2.3. Review categories and general statistics

The database used for this review was analysed in three ways: (1) Using Clarivate Analytics (Web of Science), the general statistics of citations, web of science categories, source titles (i.e. journal titles), and research areas were obtained; (2) the Bibliometix-R package (Aria and

Table 2
Number of publications on ecosystem functioning of marine benthic fauna for the top 10 web of science categories and journals.

Web of Science category	No.	Journal	No.
Marine Freshwater Biology	88	Ecological Indicators	18
Ecology	52	Marine Ecology Progress Series	16
Oceanography	49	Journal of Sea Research	13
Environmental Sciences	43	Journal of Experimental Marine Biology and Ecology	10
Biodiversity Conservation	21	Marine Environmental Research	8
Multidisciplinary Sciences	12	Plos One	8
Toxicology	8	Marine Pollution Bulletin	8
Geosciences Multidisciplinary	7	Estuarine, Coastal and Shelf Science	7
Evolutionary Biology	3	Marine Ecology and Evolutionary Perspective	6
Fisheries	3	Ecosystems	6

Cuccurullo, 2017) was also used for collecting additional information: number of publications per year, annual percentage growth rate, number of publications per country (single and multiple), and number of publications per author and; (3) information from different categories was extracted by reading each of the peer-reviewed publications included in our dataset. Although, this strategy is time consuming, it was preferred to the option provided in Clarivate Analytics, obtaining information unavailable from automated search. For example, these categories were based on the location where the studies were undertaken, in contrast with automatic sorting that uses the authors' affiliation. Publication were categorised by type of study separating; experimental manipulation, field surveys, distribution modelling, ecological modelling, meta analysis, methods, reviews and tool evaluations. Publications were also grouped by the ecosystem type where the study took place; beach, coastal, offshore (including deep sea), estuary, laboratory, mangrove, and seagrass. In another category, publications were classified according to their study organisms; macrobenthic communities as combinations of groups of multiple taxa or groups of particular taxa such as Annelida, Decapoda, Echinodermata and Mollusca. When analysing the publications, we identified that ecosystem functioning was addressed in different ways, so a classification was created to allocate each publication. As the terminology used for biological traits varies throughout the literature, a classification of traits and their modalities was performed. The variety of numerical methods for assessing ecosystem functioning was further analysed based on the publications reviewed, and sorted by their most common use (see Supplementary data Table S2). Finally, an approach category was identified; methodological approach (i.e. taxonomic diversity vs functional diversity), spatial approach (i.e. differences between sites), temporal approach (i.e. differences across time), and experimental approaches.

3. Bibliometric influence and evidence of BEF for macrobenthic fauna

3.1. Geographical and temporal spread of evidence

Investigations of marine macrobenthic fauna and their contributions to ecosystem functioning have increased due to growing interest in the

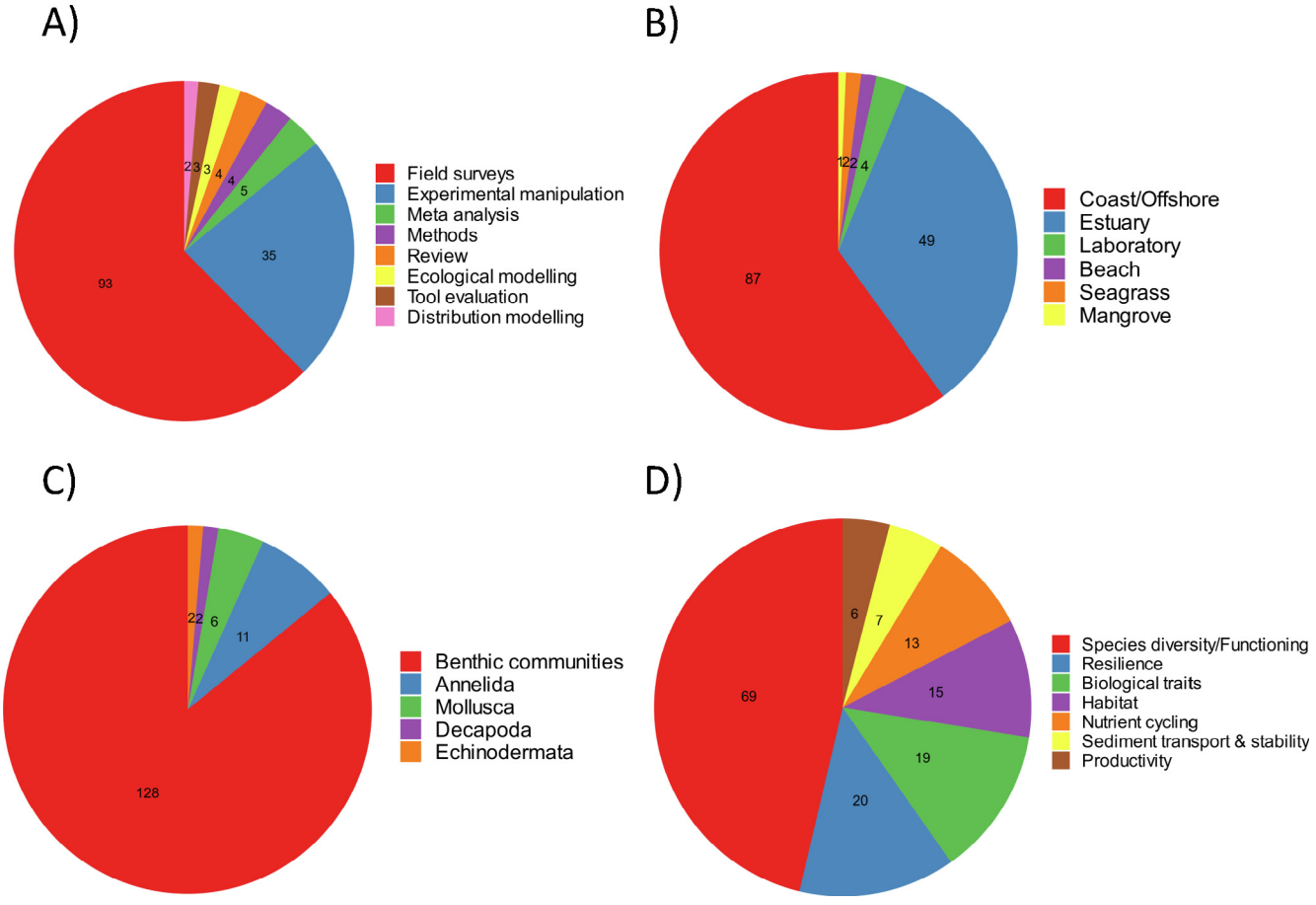


Fig. 3. Pie charts summarising the attributes found in the publications on ecosystem functioning of marine macrobenthic fauna communities. A) Number of publications per type of study. B) Number of publications per ecosystem type where the studies where performed (n = 145). C) Number of publications per taxa. D) Broad categories of ecosystem functioning that were studied. The numbers in each sector of the pie charts indicates the number of publications, with 149 papers reviewed for the analysis. For B), the ecosystem type studied could only be assigned to 145 publications.

Table 3
Approaches in assessing ecosystem functioning of marine macrobenthic fauna. Methodological: Taxonomic diversity vs functional diversity; Spatial: differences between sites; Temporal: differences across time; Experimental: manipulation of the environment and organisms.

	Methodological approach	Spatial approach	Temporal approach	Experimental approach
Number of publications (n)	30	78	26	36
Significant differences	15	70	24	36
No significant differences	15	8	4	0

field, and the value of functional perspectives for environmental decision making (e.g. Van der Linden et al., 2016). The majority of studies were performed in the Northern Hemisphere (115 publications), compared to 29 publications from the Southern Hemisphere. Only five publications had a global perspective as they included information (e.g. organisms) from multiple continents (Fig. 1A).

When publications were classified based on the continent where the studies were conducted, 62% of all publications were from Europe (93 articles), based on strong collaborations of authors from universities across Europe (e.g. Bremner et al., 2003; van der Linden et al., 2012; Norkko et al., 2013; Villnäs et al., 2018), creating networks for the advancement of ecosystem functioning of marine macrobenthic fauna. In comparison, Oceania was represented by 13.6% of the publications, followed by North America with 8.7%, while BEF was less frequently studied in South America (4.7%), Asia (4.7%), Africa (1.3%), and Antarctica (1.3%) (Fig. 1A).

A total of 29 countries had performed investigations into ecosystem functioning of marine macrobenthic fauna. Most publications on BEF, combining both single and multiple country collaborations, were from the United Kingdom (26 publications), Finland (18 publications) and New Zealand (15 publications) (Fig. 1B). Due to the high number of publications, the United Kingdom was also identified as the country that collaborates most with other countries.

Ecosystem functioning of marine macrobenthic fauna was first raised in the 1990 s, identifying traits and functions of specific macrobenthic species (e.g. Posey, 1990). However, it was not until 2002 that studies about ecosystem functioning of macrobenthic fauna included broader concepts, applicability and multiple traits per macrobenthic species (e.g. Bolam et al., 2002; Bremner et al., 2006, Bremner, 2008). In 2004–2005 no publications on this theme were recorded, but since 2005 there has been a general increase (Fig. 1C) with an average annual growth rate in publications of 9.7%. The number of citations in this research field has also grown, with a total of 3705 citations across the 17 years period (Fig. 1C).

3.2. Bibliographic analysis

Ecosystem functioning of marine macrobenthic fauna have been addressed worldwide (Fig. 1), and even though the bibliographic influence is strongly interconnected, the field is dominated by six principal authors with 10–11 publications each contributing to 41% of the publications collectively (Fig. 2A). The author collaboration network displayed four groups of interlinked collaborations (Fig. 2B). These groups reflected the strong collaboration within Europe. The co-citation network analysis based on the publications' references showed three well defined author groups based on seven central publications (Fig. 2C). These publications were often cited because they pioneered theoretical foundations about ecosystem functioning (Solan et al., 2004, Hooper et al., 2005), or stated fundamental information about macrobenthic response, including biological factors, to organic enrichment (Pearson and Rosenberg, 1978), and created or developed the methodologies for using biological traits in marine macrobenthic fauna (Chevenet et al., 1994; Bremner et al., 2003, Bremner et al., 2006, Bremner, 2008).

Publications on ecosystem functioning have been classified into different categories (Table 2). Around 31% of the publications on ecosystem functioning of marine macrobenthic fauna were primarily classified as Marine Freshwater Biology. Ecosystem functioning publications have also been categorised as ecology (18%), oceanography (17%), as well as environmental sciences (15%). Publications of marine macrobenthic fauna and ecosystem functioning were found in 46 journals. The majority of the articles were published in two research journals: Ecological Indicators (Elsevier) with 18 publications and Marine Ecology Progress Series (Inter-Research Science Publisher) with 16 publications. However, another eight journals contained a considerable number (e.g. 6–13 each) of publications in this field (Table 2).

The most frequently used terms for studying ecosystem functioning of marine macrobenthic fauna emerging through a co-word analysis from keywords are presented in a thematic map (Fig. 2D). According to Cobo et al. (2011) themes in the upper-left quadrat are highly developed and very specialized themes (e.g. functional groups, feeding guilds); in the upper-right quadrat are the motor-themes, themes well developed and important for structuring the research field (e.g. macrofauna and bioturbation); themes in the bottom-left quadrat represent emerging themes, themes that need development due to the research field is growing towards them (e.g. ecosystem functioning, ecosystem services); and themes in the bottom-right quadrat are basic themes (e.g. biological traits, biodiversity).

4. Current status of research into ecosystem functioning and functional diversity of marine macrobenthic fauna

The reviewed publications were analysed using several categories to summarise the current state of the research field. Analysing by the category 'type of study' revealed that most of the publications on ecosystem functioning of marine macrobenthic fauna were based on field surveys (62% of publications) and experimental manipulation (24% of publications) (Fig. 3A). Using the category 'ecosystem type' revealed that most of the studies were conducted on the coast/offshore, which included tidal flats and deep sea environments (56% of publications), and in estuaries with 33% of publications (Fig. 3B). Also, a large proportion of publications (68%) performed their research in subtidal environments, and only 31% of them were performed in intertidal environments (n = 136 publications). In addition, the majority of the publications were performed on soft sediments (97% of publications), and only 3% on hard bottom habitats (n = 143).

The category 'study organisms' showed that the majority of publications analysed multiple taxa (e.g. 98% of all publications), yet, a number of publications used particular groups of taxa (Fig. 3C).

Grouping the publications by the 'ecosystem function' they investigated that the majority focused on species diversity and its influence on ecosystem functioning (46% of all publications), and comparatively less publications investigated other aspects, such as those related with resilience and biological traits (13% each) (Fig. 3D).

For the category 'approach', four main directions for addressing ecosystem functioning were identified: (1) methodological approach, including publications which compared differences between taxonomic diversity and functional diversity; (2) spatial approach, referring to publications which examined differences in functional diversity between sites; (3) temporal approach, which identified publications where differences in functional diversity were assessed across time (e.g. seasons, years) and; (4) experimental approach, which included

Table 4
Most frequently used traits for the study of marine macrobenthic fauna, in the context of ecosystem functioning, encountered in the literature. Effect and response traits are presented, 'x' indicates when a trait has an influence on ecosystem functioning ('Effect'), and/or is influenced by changes in the ecosystem ('Response'). Synonyms of the traits are given due to the large variety of terms used. Some examples of modalities are provided, but there could be more in the expanded literature. The sequence of traits in the table is arranged from most to least frequent use. * refers to modalities where classes are defined depending on the aim of the study.

Traits	Effect	Response	Synonyms	Modalities
Feeding mode	x	x	Feeding	Browser
			Feeding habit	Carnivore-Omnivore
			Feeding strategy	Deep deposit feeder
			Feeding type	Deposit feeder
			Trophic mode	Dissolved matter/symbionts
			Trophic group	Filter feeder
				Filter/suspension
				Grazer/scraper
				Opportunist/scavenger
				Parasite/commensal
				Predator
				Sub-surface deposit feeder
				Surface deposit feeder
				Suspension
Mobility		x	Adult dispersal	Freely motile in/on sediment
			Adult mobility	Limited free movement
			Motility	Mobile
				None
				Sedentary
				Semi-mobile
				Semi-pelagic
				Sessile/attached
				Tubicolous
Body size	x	x	Body length	Size classes*
			Body mass	
			Individual size	
			Maximum size	
			Normal adult size	
			Potential size	
			Size	
Living habit	x	x	Adult life habit	Attached/sessile
			Habit	Burrower
				Free living
				Surface crawler
				Swimmer
				Tube dwelling
Sediment position	x	x	Environmental position	Attached to hard substrate, other structures
			Living location	Below oxygenated zone
			Living position	Epifauna
			Local habitat	Infauna
			Position in sediment	Interface
				Oxygenated zone
				Pelagic
				Profound surface
				Surface
Life span		x	Adult longevity	Age classes*
			Life duration	
			Longevity	
Morphology	x	x	Body design	Conical
			Body form	Cylindric
			Body shape	Erect
				Flat
				Flattened
				Globulose
				Hard exoskeleton
				Hard shell
				Irregular
				Rectangular
				Round
				Soft
				Soft protected
				Upright
				Vermiform
Larval type		x	Development mechanism	Direct
			Larvae	Lecithotrophic
			Larval development	Planktotrophic
				No larvae
Bioturbation	x	x	Sediment transport	Biodiffusor
			Sediment reworking	Bioirrigator
			Sediment mixing	Conveyer belt transport
				Deep mixing
				Diffusive mixing
				No bioturbation
				Regenerator
				Surface deposition
				Surface mixing
				Surface modifier
				Transport
				Upward/downward conveyor
Reproductive mode		x	Reproductive technique	Asexual
				Gonochoristic
				Hermaphrodite
				Oviparous
				Ovoviviparous
				Sexual broadcast spawning
				Sexual direct development
				Sexual ovigerous
				Sexual shed eggs
				Sexual spawning
Reproductive frequency		x	Reproduction per year	Annual
				Biennial
				Continuous
				Seasonal
Movement method		x	Type of movement	Burrowing
				Crawling
				Jumping
				None
				Swimming
				Walking
Degree of attachment		x		None
				Permanent
				Temporary
Propagule dispersal	x	x		Benthic dispersal
				Pelagic dispersal
Habitat	x	x	Habitat	Above sediment 3D structures
			Habitat creation ability	Action-sediment accretion
			Habitat structure	Action-sediment removal
				Below sediment 3D structures
				Burrow dwelling

(*continued on next page*)

Table 4 (*continued*)

Traits	Effect	Response	Synonyms	Modalities
				Creating troughs, trampling on sediment
				Forming biogenic epibenthic structures
				Form-settlement/ attached site
				Form-shelter
				Hole/pit
				Mound
				Non-permanent burrow
				None
				Permanent burrow
				Surface dwelling
				Tube dwelling
Body flexibility		x		Degrees classes*
Sexual differentiation		x		Gonochoristic
				Hermaphrodite
Indicator role		x	AMBI-Bentix	First-order opportunistic
				Indifferent
				Second-order opportunistic
				Sensitive
				Tolerant
Salinity preference		x		Oligohaline (0–5)
				Mesohaline (5–18)
				Polyhaline (18–30)
				Euhaline (30–40)
				Hyperhaline (> 40)
Sociability	x	x		Colonial
				Gregarious
				Solitary
Migration	x	x	Dispersal habit	Life stage migration
				Non-migratory
				Seasonal migration
Substratum affinity		x		Grain sediment classes*
Productivity				Low
				Medium
				High
Hypoxia sensitivity		x		Low
				Medium
				High

publications where manipulations of the environment and organisms were applied (Table 3).

A methodological approach was used in 20% of the publications. Most of these publications found a positive relationship between taxonomic and functional diversity (e.g. Bolam, 2014; Wong and Dowd, 2015), but differences between taxonomic and functional diversity emerged as well (e.g. Belley and Snelgrove, 2016; Kokarev et al., 2017). This aligns with Cadotte et al. (2011) who demonstrated that the relationship between taxonomic and functional diversity is not positive in every case. A spatial approach was applied in 52% of the publications, and most of the publications described significant differences in functional diversity between sites (Table 3; e.g. Liu et al., 2019). Only a low proportion of publications (19%) applied a temporal approach, and most of those publications found significant temporal differences (Table 3; e.g. Taupp and Wetzel 2019). Lastly, 24% of publications applied experimental approaches to their research, and all found significant relationships between macrobenthic species and sediment condition with the most common trend showing changes in nutrient cycling depending on the number and type of species involved in the experiments (e.g. Norkko et al. 2013; Thrush et al. 2017).

5. Towards unifying research on ecosystem functioning of marine macrobenthic fauna

5.1. Terminology and definitions

The research field of ecosystem functioning uses particular terminology, however, the terms used and their underlying concepts lack uniformity and robustness and in most of the cases definitions are not provided at all (Bremner 2008; Degen, 2018; Weiss and Ray 2019), leading to confusion in understanding and wrong assumptions (e.g. Macleod et al., 2008; Bolam 2014; Rezek et al., 2017). We suggest that it is imperative to specify and define the terminology used in publications, as a coherent terminology can simplify the future progression of this research field at a global scale. As a consensus for terminology, we propose definitions for key terms on ecosystem functioning of marine macrobenthic fauna, presenting Table 1 to guide further studies, based on terms most frequently used and important for assessing ecosystem functioning (e.g. Table 1; Beauchard et al., 2017; Degen et al., 2018).

5.2. Biological traits

With growing interest in BEF for marine macrobenthic fauna the complexity of trait categories used has increased (Bremner, 2008, Beauchard et al., 2017). The majority of publications analysed relied on biological traits to assess macrobenthic fauna (78% of publications, or 115 publications). We identified that 129 publications used biological trait categories, and 10 of 26 were the most frequently used. Out of the biological traits most often used in publications, feeding mode was the most frequent trait (87% of publications), followed by mobility, body size and living habit (60.5%, 58% and 56% of publications respectively).

Considering that the selection of biological traits will always depend on the specific objectives of any particular study (Reiss et al., 2009), multiple biological traits have been identified through our dataset (Table 4). In some cases, different traits have been proposed, but with the same theoretical meaning as already established traits (e.g. Tornroos et al., 2013; Darr et al., 2014, synonyms in Table 4), resulting in a lack of consistency across publications. For a better comparability and coherent understanding of biological traits, it is necessary to use a standardized framework of biological trait categories. Some examples are the framework proposed by Bremner et al. (2003; 2006); Beauchard et al. (2017) which is not specific to macrobenthic fauna; Degen et al. (2018) which is specific to polar oceans; or the one we propose in Table 4, where traits are specified along with their synonyms (different theoretical meaning found through the literature), and the categories or modalities, providing a robust baseline for the standardization of the research field.

Another issue emerging from our literature review is the procedure for the selection of biological traits, as most of the publications used only those traits where information was available for species studied. Quantitative methods for choosing traits and weighting traits have been developed (Petchey and Gaston 2006), however refinement of traits is still needed. For many species of marine macrobenthic fauna, knowledge gaps on their biological and ecological information complicate biological trait allocation. In addition, due to the lack of identification keys for many benthic macroinvertebrates, studies with varying levels of taxonomic resolution and the inclusion of morphospecies make selection of biological traits even more difficult (Bremner, 2008, Beauchard et al., 2017; Degen et al., 2018). Recently, Weiss and Ray (2019) proposed a standardized method when selecting biological traits, providing a guide to support functional ecological comparisons across taxa. However, further research using such an approach still needs to be done to verify its validity.

Table 5
Frequently used measures to assess of ecosystem functioning on marine macrobenthic fauna encountered in the literature. Rank; A: Suggested by the authors based on the outcomes from the research weaving analysis; B: According to number of appearances in the publications analysed.

Rank		Name	Id	Description	Formula	Source
A	B					
1	8	Functional diversity	FD	Four steps are required: (i) obtaining a trait matrix, (ii) transform the first matrix into a distance matrix, (iii) create a dendrogram clustering the distance matrix, and (iv) calculate the total branch length of the dendrogram.	$FD = i^{'}.\ h2$	Petchey and Gaston (2002), Mouchet et al. (2010).
2	7	Rao's quadratic entropy	Q	Sum of pairwise distances between species weighted by relative abundance.	$Q = \sum_{i-1}^{S-1}\sum_{j-j+1}^{S-1} dijpipj$	Rao's (1982), Champely and Chessel (2002), Mouchet et al. (2010).
3	15	Functional Richness	FRic	The amount of functional space occupied by a species assemblage; Convex Hull Volume.	Quickhull algorithm	Mason et al. (2005), Villeger et al. (2008), Mouchet et al. (2010).
4	13	Functional Evenness	FEve	The evenness of abundance distribution in a functional trait space.	$Feve = \frac{\sum_{i=1}^{S-1}\min\left(PEWi, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1-\frac{1}{S-1}}$	Mason et al. (2005), Villeger et al. (2008), Mouchet et al. (2010).
5	17	Functional divergence	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance.	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta \mid dl + dG}$	Mason et al. (2005), Villeger et al. (2008), Mouchet et al. (2010).
6	10	Functional redundancy	FR	Ratio between FD and H'.	$FR = FD/H'$	de Bello et al. (2007), van der Linden et al. (2012).
7	16	Functional dispersion	FDis	Abundance-weighted mean distance of individual species to their group centroid (all species community) in multivariate trait space.	$FDis = \frac{\sum ajzj}{\sum aj}$	Laliberté and Legendre (2010)
8	5	Fuzzy Correspondence Analysis	FCA	Fuzzy coding approach, scoring species according to their biological traits. A fuzzy variable takes values of type a = (a1, … , ak) giving the importance of k categories.		Chevenet et al. (1994), Bremner et al. (2006).
9*	3	Biological Trait analysis	BTA	Three numerical matrices are required: (i) taxa abundance in each site; (ii) biological traits of the taxa; and (iii) the combination of the previous two matrices.		Statzner et al. (1994), Bremner et al. (2003).
10	12	Community Bioirrigation Potential	BIPc	Abundance and biomass data with information about the life traits of individual species or taxonomic groups	$BPc = \sum_{i=1}^{n}\sqrt{\frac{Bi}{AixAixMixRi}}$	Solan et al. (2004), Queiros et al. (2013).
11	6	Shannon diversity Index	H'	The proportion of species *i* relative to the total number of taxa (p_i) is calculated, and then multiplied by the natural logarithm of this proportion (lnp_i)	$H^{'} = -\mathrm{K}\sum_{i=1}^{R} pi\log pi$	Shannon (1948), Spellerberg and Fedor (2003)
12	9	Pielou's index	J'	quantifies how equal the community is numerically	$J^{'} = \frac{H^{'}}{H^{'}max}$	Pielou (1966)
13	2	Abundance	A	Number of organisms found in sample.	–	–
14	1	Taxonomic diversity	S	Number of taxa found in a sample.	–	–
15	4	Biomass	B	Ash-free Dry Weight (AFDW).	–	–

*BTA is a measure required to calculate other functional metrics.

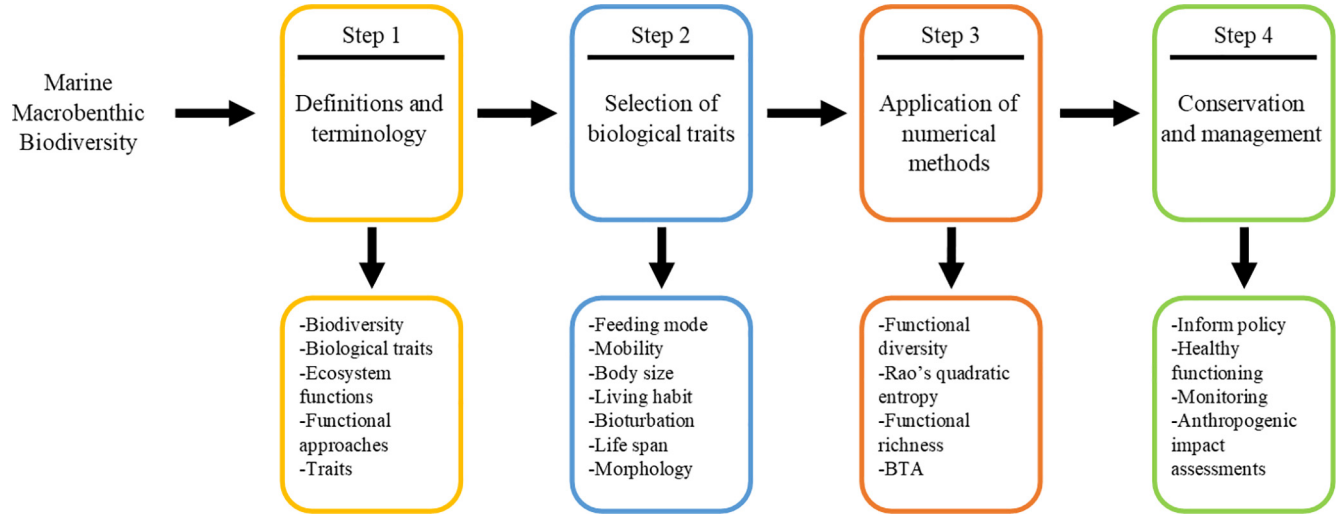


Fig. 4. Conceptual step-by-step guide for assessing ecosystem functioning of marine macrobenthic fauna.

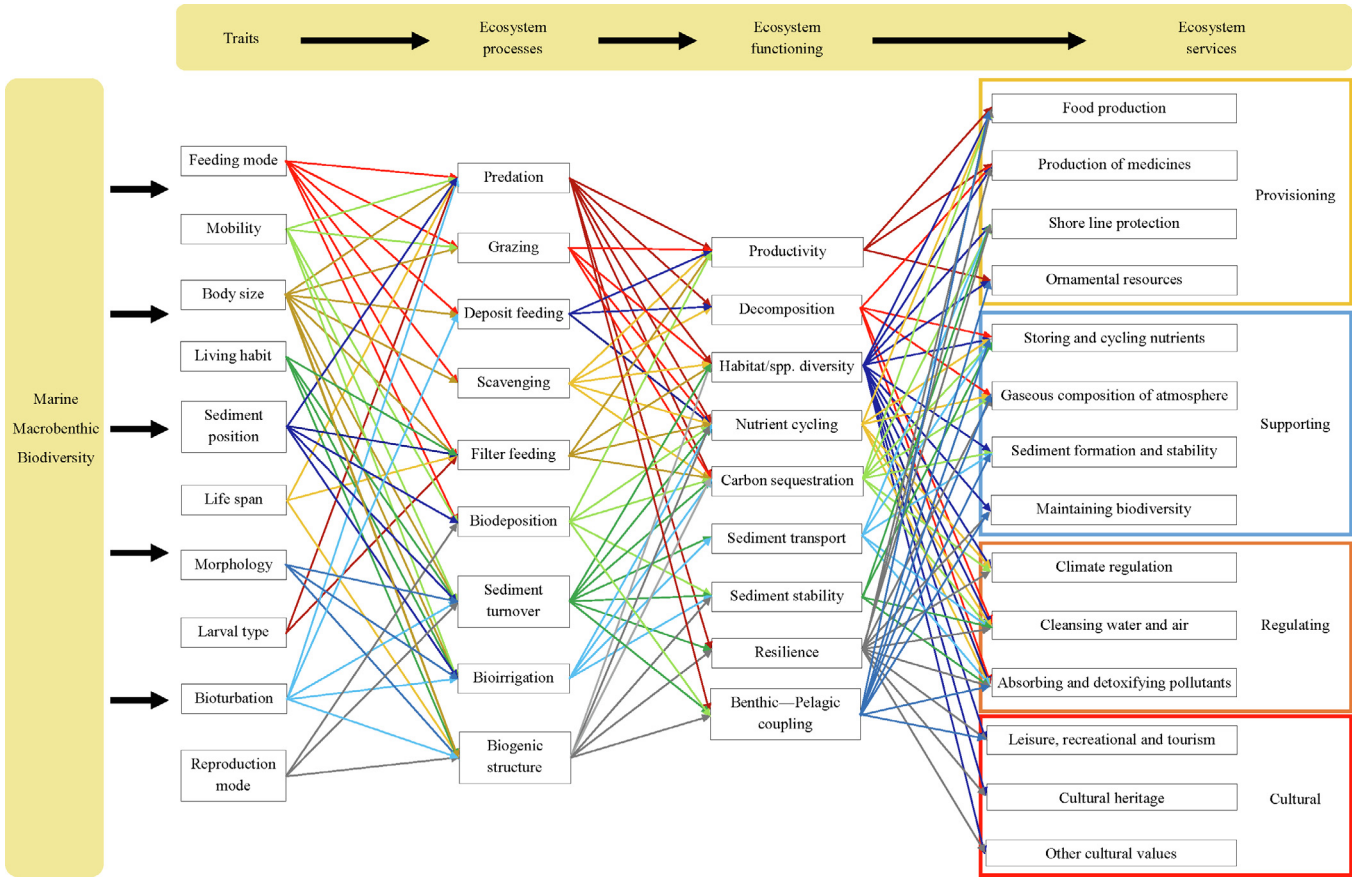


Fig. 5. Interlinkages among biodiversity of marine macrobenthic fauna, traits (the ten most frequently used, see Table 2), ecosystem processes, ecosystem functioning and ecosystem services. Note that this multi-ecosystem linkage is not restricted and can include other traits, processes, functioning and services in the expanded literature. Information was collated from: Norling et al., 2007; Bremner, 2008; Townsend et al., 2011; Norkko et al., 2013; Queiros et al., 2013; Snelgrove et al., 2014; Song et al., 2014; Clare et al., 2015; Frid et al., 2016; Weigel et al., 2016; Beauchard et al., 2017; Thrush et al., 2017; van der Linden et al., 2017; Dissanayake et al., 2018; Liu et al., 2019.

5.3. Consistency in numerical methods

A large variety of methodologies and approaches for addressing ecosystem functioning of marine macrobenthic fauna has been identified (e.g. van der Linden et al., 2012; Belley and Snelgrove, 2016; Gusmao et al., 2016; Baldrighi et al., 2017). Out of all publications, 86% used at least one numerical method to assess ecosystem functioning out of 39 different numerical metrics which were applied in the reviewed publications. However, only 17 numerical metrics were found in more than five publications (see Supplementary Data Table S2 for a full list). The numerical methods more recurrently used as a proxy for ecosystem functioning were taxonomic diversity (65 publications), abundance (59 publications) and biological traits (56 publications), taking into consideration that in the majority of the publications a

combination of multiple numerical methods was used.

The variety in numerical methods found across studies was due to differences between authors, geographic areas, taxonomic groups and study type. Applying several metrics to measure how an ecosystem functions is not always practical. The wide variety of methods used, and the lack of accurate definitions that we identified across the publications, revealed the need for consistency to measure ecosystem functioning. For example, some publications used taxonomic diversity and abundance as a measure for ecosystem functioning (e.g. Lohrer et al., 2010; Pratt et al., 2015), whereas functional diversity was found less often, although functional diversity is the key component of biodiversity for reliably studying ecosystem functioning (Hooper et al., 2005; Wright et al., 2006; Legras et al., 2018).

To avoid misinterpretations in the fast-growing field of BEF research on marine macrobenthic fauna, it is imperative to standardize the metrics and methods used. Therefore, we suggest following the most important and previously established methodological frameworks when assessing ecosystem functioning (Table 5). Otherwise, results from different studies and geographical areas cannot be reliably compared, which may mask significant information or lead to wrong conclusions (Petchey and Gaston, 2006; Bremner, 2008; Snelgrove et al., 2014).

6. Outlook

With ecosystem functioning of marine macrobenthic fauna growing as a research field, our analysis revealed the complexities of multiple methodologies and usage of terminology, creating discrepancies across publications. Such inconsistencies limit the potential of comparing and exploring study outcomes between different geographical areas.

Here, we provide a conceptual step-by-step guide on approaching ecosystem functioning for marine macrobenthic fauna (Fig. 4). The following steps are imperative for advancing the research field: (1) Defining the terminology used in each publication to avoid misinterpretations and wrong conclusions. Although most of the terms are widely used, a global consensus on their definitions for ecosystem functioning in marine macrobenthic fauna is lacking. To facilitate more consistent use of terminology, we propose to use the definitions presented in Table 1.

(2) Selection of biological traits that are most suitable to address the study aims, based on species information available and previously standardized frameworks. The overview presented in Table 4 can be used as a standardised resource base for information about traits, synonyms, traits-modalities, and whether traits can indicate an effect or a response at ecosystem level (see also Beauchard et al., 2017; Degen et al., 2018; Weiss and Ray, 2019).

(3) We recommend that numerical methodologies should follow an ordered system, prioritizing the use, at least, of one of the top six measures to assess ecosystem functioning (see ranks A in Table 5). Of those measures, functional diversity is the most relevant for understanding the links between ecosystem functioning and marine macrobenthic fauna.

(4) Outcomes from ecosystem functioning assessment can be used as valuable tools for informing conservation policy and management of natural ecosystems.

We also suggest, for a full understanding of how an ecosystem is functioning, to develop more specific approaches, where the complex interlinkages across traits, ecosystem processes, ecosystem functions and services are considered. Single or multiple traits can influence several ecosystem functions, or one ecosystem function could be affected by several traits. For example, body size as a biological trait category influences several ecological processes such as predation, scavenging and bioturbation, which can then affect single or multiple functions in the ecosystem (e.g. productivity, nutrient cycling and sediment transport) and, depending on the ecosystem functions involved, one or more ecosystem services (Fig. 5).

7. Concluding remarks

In this review, we presented the first ecological synthesis that uses the approach of research weaving for analysing the ecosystem functioning and functional diversity of marine macrobenthic fauna. Thus, we provide a detailed description of the influence and evidence of the current knowledge of ecosystem functioning in marine macrobenthic fauna.

The analysis revealed that advances in this research field are challenged by multiple knowledge gaps, several different theoretical ideas, terminology and methods used. The patchiness in research globally further indicated that BEF for benthic communities is understudied in many geographical areas. The heterogeneity in terminology, lack of consistency in selection of biological traits, and inconsistencies in numerical methodologies, making it difficulties to extrapolate and compare findings on ecosystem functioning of marine benthic ecosystems, potentially leading to wrong conclusions. Therefore, we have proposed a conceptual guide suggesting the use of standardized terminology, selection of biological traits and numerical methodologies. We also emphasize the need to address the complex interlinkages between biological traits, ecological processes, ecosystem functions and services, to improve our understanding and management of these ecosystems.

With the advancement of technology, and with the willingness to expand established worldwide collaborations and research networks, the availability of information and resources (e.g. trait databases, methodologies) in this research field will only increase. However, consensus on standardised approaches is mandatory for reducing the knowledge-gap in ecosystem functioning of marine macrobenthic fauna on a global scale.

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Author's contributions

OLG conceived the ideas and developed the outline for the manuscript. All authors designed the methodology and collected the data. OLG analysed the data, prepared the figures and tables. All authors contributed critically to the manuscript draft and gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106379.

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