Assessing sea floor functional biodiversity and vulnerability

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ABSTRACT: The marine benthos has been largely studied through the use of response traits that characterise species vulnerability to disturbance. More limited has been the specific use of effect traits that represent other species descriptors and that express ecosystem functions. On the sea floor, the benthos is a key ecosystem-engineering component for which functions can be relevantly derived from effect traits. This study provides a typology of sea floor functions based on an extensive data compilation of effect traits. We classified 812 benthic invertebrate species from the northeast Atlantic by 15 effect traits expressing substratum alteration and habitat creation. Cluster analysis identified 15 species groups that represented various epi- or endobenthic functions. Beyond function–habitat specificity, we show that soft sediment species exhibited broader functional niches in the trait space that increase multi-functionality, and were endowed with rare combinations of traits that expanded the functional extent of the species assemblage. As a consequence, soft sediments can host a higher functional diversity than hard substrata because a wider range of above- and below-substratum activities are possible in soft bottoms. Based on response traits documented for the same species and used to express vulnerability to natural or human-induced disturbance, we then show that vulnerability within sea floor functions can be considerably variable. This can be a consequence of the independence between the evolutionary nature of response traits and the contingent engineering abilities of benthic species through effect traits. The paper provides theoretical and utilitarian clarifications on this trait dichotomy.

KEY WORDS: Benthic invertebrate · Effect trait · Ecosystem engineering · Ecosystem function · Functional group · Functional diversity · Vulnerability

1. INTRODUCTION

The sea floor hosts the majority of marine species, occupies the largest single ecosystem on Earth by area and has been extensively disturbed following centuries of fishing, among many other anthropogenic pressures (Snelgrove 1999, Snelgrove et al. 2014). However, most biological conservation studies have focussed on species vulnerability (e.g. life span; Rijns- dorp et al. 2018), without distinguishing between the functions species perform in the marine ecosystem (e.g. bioturbation; Kristensen et al. 2012). It is therefore unclear whether protecting vulnerable species conserves sea floor ecosystem functions, since species survival and ecosystem function are not necessarily expressed by the same traits (Díaz & Cabido 2001, Lavorel & Garnier 2002). Among the numerous studies using a large variety of traits, there is still a lack of

clarification regarding the type of traits to use for one research objective or another. While facing a still growing literature in marine benthic functional ecology, it is necessary to come back to the essential question of how to consider a species in an ecosystem.

A species can be described under 2 different perspectives related to mechanisms underpinning species assembly. The first is the Darwinian concept of fitness (growth, survival and reproduction), whereby biological performances of individual organisms are selected by abiotic forces and direct biotic interactions (environmental filtering and limiting similarity, respectively; Weiher & Keddy 1995). The second, ecosystem engineering (Jones et al. 1994), is the result of fitness expression of an engineering species (Table 1) as an effect on the fitness of another species by modulating resource availability, either directly (autogenic engineering, e.g. habitat creation through reef building) or indirectly (allogenic engineering, e.g. increasing oxygen concentration through bioirrigation or decreasing through respiration). Hence, a species can be considered based on traits that express fitness and those that express ecosystem engineering (Table 1). These 2 categories of traits are respectively called 'response' and 'effect' traits (Lavorel & Garnier 2002). The distinction between these traits is not always clear, as some traits can fall under both categories. As an example, coral morphology can have prominent habitat effects on other species, but arborescent forms are very sensitive to physical disturbance, so morphology can also express survival. If we now consider burrowing species, the survival (i.e. escaping physical surface pressure) can also be expressed through their burrowing response, with consequent bioturbative effects.

Ecosystem engineering is considered as a second paradigm since the same combination of response traits (i.e. life strategy) can give rise to various types of engineering (Jones et al. 1994, 1997). It is a truism that species evolve ultimately to achieve reproductive success, not ecosystem engineering. Whereas response traits evolve through natural selection induced by environmental forces, there is no clear evolutionary determinism of ecosystem engineering based solely on response traits (Odling-Smee et al. 2013, Matthews et al. 2014). For instance, environmental stress or habitat disturbance frequency can select organism growth rate and associated reproductive functions (Southwood 1988), with similar selective processes known in very different clades of the living world (Grime & Pierce 2012). By contrast, predicting engineering type from selected response traits can be highly context-dependent (Lavorel &

Garnier 2002). In the marine benthos, burrowing ability constitutes an exception, as it expresses both response and effect: a 'burrowing revolution' took place during the Cambrian era in response to predation (Meysman et al. 2006b), which represents a causal relation between ecosystem engineering and fitness. However, this holds only at the macro-evolutionary level, and at present there is no causal relation at a finer level between key response traits such as life span and burrowing depth or burrow type, since burrowing can also be associated with various trophic requirements (Fauchald & Jumars 1979), another fitness opportunity than surviving. As a consequence, the engineering ability of a species is contingent upon the unpredictable ecological opportunities for the fitness components met or not over evolutionary time (Pickett et al. 1994). Furthermore, the engineering ability of a species can evolve only when it has positive feedback on the fitness of this species ('extended phenotype'; Dawkins 1982, Odling-Smee et al. 2013). From there, since vulnerability to disturbance depends on response traits, any degree of vulnerability may be expected in benthic ecosystem functions.

This response–effect trait duality is critical to consider, yet it has rarely been considered in marine benthic ecology (Villnäs et al. 2018), whereas the nature of traits is intrinsic to research purposes. Ecosystem engineering is an internal force of the species assemblage, changing diversity mechanistically through effect traits, whereas diversity responds to external forces (e.g. storm- or human-induced disturbance) through response traits, indirectly affecting engineering. While effect traits could also respond to human-mediated disturbance, this should be indirectly following impact on the fitness of the engineer, such as in the case of slow growth preventing population recovery and consequently engineering recovery (Oliver et al. 2015). Thus, the dual use of response and effect traits as part of benthic impact assessment should be conducted following 2 steps. Firstly, at the species level, an engineering ability must be defined solely through effect traits, including those that could express both effect and response. Then, at the assemblage level, the range of response trait performances from the different species endowed with this ability should be used to assess its vulnerability. Much effort has been devoted to the development of indicators of species vulnerability to disturbance based on response traits (Tyler et al. 2011, Beauchard et al. 2017), while the assessment of benthic ecosystem engineering vulnerability remains largely unresolved. This repre-

Table 1. Definitions of key concepts

Concept	Definition
Response traits	Every characteristic of an organism related to fitness components (growth, survival and reproduction). These traits respond to environmental forces, abiotic and biotic, that select organisms within habitats. They are the products of evolution through environmental filtering (abiotic constraints) or organism interactions that push organisms toward specific life strategies as selected combinations of traits (Stearns 1992). These traits are primarily species properties; they do not directly express ecosystem functions (Schmera et al. 2016), but they enable assessment of the vulnerability of a species to a given stress or disturbance.
Effect traits	Traits describing the effects of an organism on habitat properties as a result of fitness expression, such as physiological activity, space occupation, moving, foraging or sheltering (Lavorel & Garnier 2002). They primarily express ecosystem function.
Ecosystem engineering	Alterations of the environmental conditions by an organism (the 'engineer') that directly or indirectly modulate the availability of resources to co-occurring organisms (Jones et al. 1994). These effects can be expressed by effect traits. Indistinctly, the fitness of co-occurring organisms can be positively (e.g. refuge creation) or negatively impacted (e.g. hindrance).
Ecosystem function	Any ability of abiotic and biotic components that contributes to the flow of energy and materials in an ecosystem (Díaz & Cabido 2001). Hence, this includes species interactions (e.g. predation, competition) and ecosystem engineering.
Sea floor function	Ecosystem function ensured by abiotic or biotic sea floor components, such functions being necessarily and intrinsically linked to the substratum (Snelgrove et al. 2014, 2018). Biotic components include microorganisms (biogeochemical functions), fauna, seaweeds and phanerogams that fulfil comparable functions (e.g. habitat creation, biostabilisation; Ólafsson 2017). Sea floor functions concentrate most of marine ecosystem engineering, and contribute to energy fluxes through secondary production and species interactions. They can be represented by groups of benthic species endowed with similar effect traits and that can ensure full functions (e.g. emergent structure of a coral providing refuge), partly (e.g. partial carbon mineralisation along the diagenetic process) or different functions.
Functional diversity	Amount of variation between organisms positioned in a Euclidean space defined by their traits and where it can be measured in different ways (Mouillot et al. 2013). It is not necessarily correlated to species richness and represents an irreplaceable way to assess ecosystem structure and function (Villéger et al. 2008). Based on response traits and mean distance between species, a high value of habitat functional diversity can indicate different states of vulnerability in a species assemblage (e.g. mix of resistant and vulnerable species), as well as a low value (e.g. only vulnerable or only resistant). Based on effect traits, by contrast, a high value generally indicates co-occurring non-redundant functions, important for the functioning of the entire ecosystem.

sents a critical knowledge gap, because it is not yet clear if the protection of only the most vulnerable species to human pressures is sufficient to preserve ecosystem functioning.

Here, we consider 'sea floor function' as a combination of benthic effect traits that express ecosystem engineering (Table 1), which include services beneficial to the ecosystem (e.g. habitat creation) as well as services beneficial to humans (e.g. carbon sequestration) (Díaz et al. 2013, Snelgrove et al. 2014). Ecosystem engineering has been historically a major focus in marine zoobenthic ecology, especially in soft bottoms, whose malleable nature enables various physico-chemical processes to occur (Pearson & Rosenberg 1978, Solan et al. 2004a, Middelburg 2018). In hard substrata, habitat creation has been a leading research endeavour, especially reef-building

in corals and in other sessile and colonial organisms (Ballesteros 2006, Rossi et al. 2017). However, the literature is still lacking exploratory and comparative works considering a wider panel of sea floor functions and diversity (e.g. both bioturbation and habitat creation) from various substrata. In terrestrial and aquatic ecology, the concept of species functional groups has been a popular way to deal with large numbers of species when comparing ecosystems by simplifying differing assemblages using a limited number of comparable functions. Gérino et al. (2003) and Pearson (2001) were pioneers in marine benthic ecology, classifying benthic species into typological groups according to their relations with the sediment. Later, Queirós et al. (2013) provided the most comprehensive data compilation on species sediment mixing types in terms of taxonomic coverage.

However, these classifications are limited to species in soft sediments, and attribute a dominant function to each species, whereas the functional role of a species can be manifold. For instance, a large walking crab can generate substantial diffusive mixing at the sediment surface while inducing regenerative mixing when hiding (Solan et al. 2004b). Likewise, mussels are organised in reefs that provide refuge or permanent habitat to many species, and the dead shells can remain for hundreds of years at the surface of the sea floor, continuing to offer habitat opportunities to many organisms (Gutiérrez et al. 2003); in addition, suspension feeding ensures the transfer of suspended matter to the sea floor.

What has been missing is a reference framework to draw on the use of multiple effect traits to address fundamental and critical questions on the functional structure and vulnerability of species communities. Moreover, the species assemblage generally represents a central focus when assessing diversity and vulnerability, whereas another level of diversity has been largely ignored in marine studies. Indeed, the species level can also represent a structurally variable unit in the multivariate trait space, and can be crucial for detecting the functional importance of an assemblage, even one that is species-poor. For instance, the functional niche reflects the spread of trait modalities of a species within the trait space (Rosenfeld 2002). The larger the niche breadth, the greater is the species' functioning potential; Violle & Jiang (2009) defined it as the 'impact niche', in opposition to the more traditional Hutchinsonian concept of 'requirement niche' based on fitness components (Hutchinson 1957). Thus, expressed by effect traits, niche breadth reflects the concept of 'multi-functionality' defined by Snelgrove et al. (2014) as the contribution to more than one ecosystem function. Functional originality (Kondratyeva et al. 2019) is another concept synonymous with distinctiveness or uniqueness, measuring the rarity of a trait combination that could denote peculiarities in some species independently of their abundance and that could raise conservation interest (Pavoine & Ricotta 2021). Whereas traditional diversity indices at the level of the assemblage indicate the level of species dissimilarity (Table 1), the concomitant use of species level-indices can bring complementary knowledge on species multi-functionality for assemblages of equal average species dissimilarity.

We propose such a framework based on an extensive compilation of effect trait data of the European macro- and mega-zoobenthos from which we derived a typology of sea floor functions as species groups and species structural properties in the trait space. Through an exploratory data analysis, we provide a general mechanism to explain, from the species to the community level, variations in sea floor functional diversity along habitat gradients. We use broad species environmental preferences (habitat traits) to generate such gradients and test hypotheses at the biogeographic scale regarding α- and β-diversity (within- and between-habitat, respectively). As both species and functional composition are expected to depend on substratum type, we hypothesised significant associations between habitats and functions (H_1). Given the broader spatial occupation of soft sediments by fauna (i.e. above and below the substratum), we hypothesised that soft sediment habitats should exhibit a higher functional α-diversity (H_2), hence ensuring potentially more ecosystem services (Snelgrove 1999). Lastly, we provide a quantification of sea floor function vulnerability through the use of response traits. According to the possible independence between fitness and ecosystem engineering (Lavorel & Garnier 2002), we hypothesised that sea floor functions are equally vulnerable to disturbance (H_3). This work brings insights at the continental scale, and expectations at smaller scales are discussed. In doing so, we aimed to provide a new large-scale data set covering both hard and soft substrata across the northeast Atlantic, provide a framework that distinguishes between response and effect traits to explore patterns in functional diversity, and show how this trait information can be used to inform management decisions.

2. MATERIALS AND METHODS

2.1. Trait data

We documented traits of 812 species found in European waters and belonging to the typical phyla found in benthic studies (Fig. 1, Table 2); a few non-native and abundant species were also considered (e.g. *Marenzelleria viridis*). Effect traits were solely used to derive sea floor functions and species structural properties in a first exploratory data analysis. Then, whereas the response–effect trait duality was of major importance for testing H_3, our analyses took place at the biogeographic scale using environmental information at the species level in order to derive general habitats as combinations of depths and substrata (see Section 2.1.2). Therefore, effect and habitat traits were used to test H_1 and H_2, and effect and response traits were used to test H_3.

Arctic (Arc)
Northern European Seas (NES)
Lusitanian (Lus)
Mediterranean Sea (MS)
Black Sea (BS)

Fig. 1. Biogeographic context including the 5 European provinces in which species documented for traits occur. Colour bar shows the corresponding depth (m). White and black contour lines: 200 and 4000 m isobaths, respectively. Dashed lines: biogeographic delineations from Spalding et al. (2007). For species occurrences, see Table S1.1
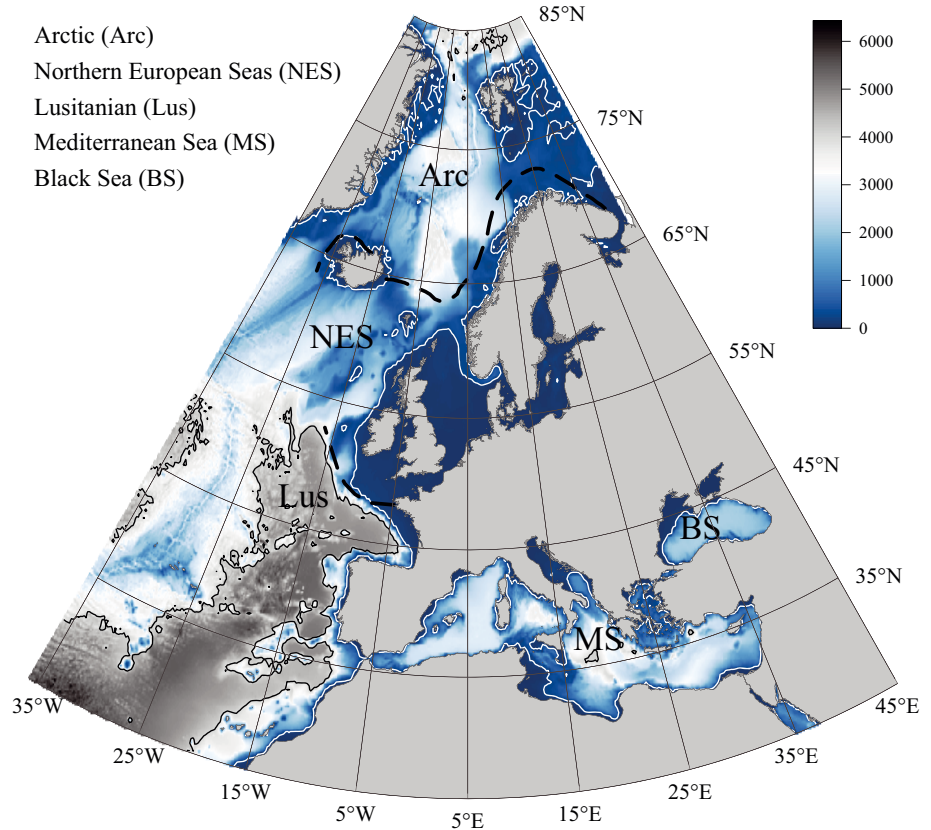
Although traits represent the major focus in species descriptions, they are not elementary units, as they can take several states, usually called 'modalities' that are the functional descriptors to be quantified within a trait. This concept was popularised by Chevenet et al. (1994), who proposed 'fuzzy coding'

Table 2. (a) Species counts per biogeographic province and depth category and (b) number of species in common between provinces. Arc: Arctic; NES: Northern European Seas; Lus: Lusitanian; MS: Mediterranean Sea; BS: Black Sea; see Fig. 1. For depth categories, shore: 0–20 m; shelf: 20–200 m; deep: >200 m

| | Province | | | | | |
	Arc	NES	Lus	MS	BS	Total
(a) Depth						
Intertidal	103	261	250	192	54	302
Shore	182	512	498	438	103	637
Shelf	156	381	371	329	70	477
Deep	89	140	143	128	22	191
Total	243	627	615	543	121	812
(b) Province						
NES	220					
Lus	144	508				
MS	96	399	490			
BS	33	102	115	118		

as a generic method for trait quantification and analysis. Fuzzy coding consists of attributing scores of species affinity for a given modality based on measurements from the literature, where 0/1 represents a basic scoring in the absence of quantitative information (e.g. distribution of body size), larger intervals enabling a more accurate quantification whereby several modalities receive a score of variable importance. For instance, a species that usually occurs at a body length of 9–10 cm can be coded for the modality profile <3/3–10/>10 as 0/3/1 if few individuals exceed 10 cm, 0/3/2 if this applies to some, or 0/3/3 if this occurs regularly. In the case of qualitative modalities (e.g. 'epi-bioconstruction type'; Table 3) equally present, the same score is attributed. We used a 0–3 scoring that enabled us to distinguish a low affinity for a given modality (1) from a high affinity (3). Scores were then expressed as proportions of profile total sum (i.e. 0/3/1 becomes (0.00/0.75/0.25). In some cases, we used genus-level information where species-level information was not available. The documentation, totalling 2473 references, was primarily based on peer-reviewed articles (2276), complemented with books (73), academic theses and dissertations (61), reports (54) and websites (9) (Supplement 1; see www.int-res.com/articles/suppl/m708 p021_supp/ for all supplements).

Table 3. Description of the species effect traits used to derive sea floor functional gradients and species groups in the multiple factor analysis

Trait	Modality	Information
Substratum depth distribution	0 0–5 5–15 15–30 >30	Main substratum depth where the organism is encountered (in cm). Not directly expressive of engineering. Indicates where the engineering is mostly realised. A burrowing organism does not constantly lie in the deepest part of its burrow.
Biodiffusion	Null Low High	Random dispersion of sediment particles by burying/burrowing organisms.
Downward conveying	Null Low High	Downward displacement of sediment particles; also defecated materials, although not specifically.
Upward conveying	Null Low High	Upward displacement of sediment particles, mostly through burying action.
Regeneration	Null Low High	Instantaneous downward and upward sediment particle displacement; generally encountered in crabs.
Bioerosion	None Scarring Scraping/Perforating Boring	Erosion of hard substrata through grazing (e.g. urchins) or settlement and growth (e.g. barnacles). Stronger effect through boring.
Biodeposition	Null Low High	Pelagic–benthic sediment transfer through suspension feeding. Part of 'benthic–pelagic coupling'. Function of the degree of suspension feeding and organism biomass.
Biostabilisation	Null Low High	Mitigates sediment erodibility through hydrological modulation (e.g. zoic tubes, mounds, reefs).
Ventilation/Pumping	Null Low High	Ability to generate water fluxes into the substratum through body or appendix undulations. Expresses bioirrigation magnitude when considered with endo-bioconstructions depth and burrow width.
Burrow width	None Narrow Intermediate Wide	Considered with Ventilation/Pumping and endo-bioconstruction depth, expresses bioirrigation magnitude and endo-benthic habitat creation; <5, 5–10 and >10 mm, respectively.
Endo-bioconstruction type	None Rugosities/Pit Chimney/Funnel Tube IJ-shaped burrow UY-shaped burrow Branched burrow Anastomosed burrow	Chimney/Funnel provides a respiratory function (e.g. *Echinocardium* sp.). Tube is a construction from organic or mineral materials. UY-shaped burrow differs from IJ-shaped by enhancing water flux through bioirrigation. Respectively, the same between anastomosed and branched burrows, both generally deep structures.
Endo-bioconstruction depth	None 0–5 5–15 15–30 >30	Endobenthic vertical effect size in cm, specifically semi- or permanent burrows.
Epi-bioconstruction type	None/Surficial Mat Mound Tube/Tubular protrusion Shell Stalk/Feather Protuberance/Lobe Arborescence	Type of epibenthic structure of the individual organism. Mat, soft or hard, generally flattened. Mound specific to soft sediment. Shell, although possibly endobenthic, can be surfaced through physical disturbance. Stalk/Feather generally encountered in corals. Protuberance as simple protrusion, but can be important refuge if extended as a complex structure, e.g. goose barnacle.
Epi-bioconstruction extension	None Simple Horizontally flattened Horizontally erect Vertically complex Vertically highly complex	Isolated/Clumped for spatially limited organism construction (e.g. isolated barnacles, sea pens). Others: from mostly horizontal extension (e.g. spionid tube lawn) to more vertically structured reef (e.g. from mussel to oyster and coral reefs).
Epi-bioconstruction size	None <1 1–3 3–10 10–20 20–50 >50	Largest dimension between horizontal and vertical extent (in cm). Type of extent specified by epi-bioconstruction extension. If an organism is generally encountered aggregated, this is the size of the aggregation (e.g. mussel reef) rather than the size of the individual body length (e.g. shell).

Whereas the studied fauna (macro- and mega-benthos) includes several thousand species (Coll et al. 2010, Narayanaswamy et al. 2010, Bodil et al. 2011), we considered the representativeness of the documented set of species based on 3 strong assumptions: (1) among 11 documented phyla, we documented the most functionally extreme and uncommon living forms so that the range of represented functions would encompass the functionalities of species that were not documented; (2) the most documented species are generally the most abundant or those exhibiting the most peculiar trait combinations that have raised scientific interest; (3) functions of closely related species are often closely related. Importantly, here we focus more on which functional types occur rather than how many species are represented per functional type.

2.1.1. Effect traits

We defined 15 effect traits that directly or indirectly express various sea floor functions (Table 3). These functions include different kinds of sediment alterations: sediment mixing types, biodeposition, biostabilisation and bioerosion. Sediment mixing (i.e. biodiffusion, upward and downward conveying, and regeneration) was quantified differently from what is usually encountered in the literature. It cannot be expressed by a single trait, as 2 aspects, namely affinity for mixing type and mixing magnitude (i.e. amount of sediment displaced per time unit), must be considered separately for each mixing type. We used body mass, mobility and affinity scores for calculating mixing types as 4 distinct traits; Supplement 2 provides detailed descriptions of trait documentation and calculation. Other traits were considered as part of habitat creation through 'bioconstruction' (Ingrosso et al. 2018), which is not restricted to the substratum surface. Indeed, large burrows are known to host a variety of commensal, symbiotic, opportunistic and foraging organisms, including fish (Woodin 1978, Lackschewitz & Reise 1998, Callaway 2006, Tseng et al. 2019).

2.1.2. Habitat traits

In order to test our hypotheses, we defined general benthic habitats based on species preferences as habitat traits. Various descriptors can be used to characterise benthic invertebrate habitats. Given its major importance in determining species composition, we considered substratum, firstly from hard to soft substrata, but also between soft sediment types

(Snelgrove & Butman 1994). Water depth is another key descriptor along habitat gradients and zonation, as it modulates light availability and stratification, and consequently the availability of pelagic resources (Etter & Mullineaux 2001). Six categories of substrata were considered: 'Hard' (rock, stones, pebbles), 'Mixed hard–soft' (any previous category with any of the following ones), 'Gravel', 'Sand', 'Muddy sand' and 'Sandy mud–Mud'. Water depth was divided into 4 categories: 'Intertidal', 'Shore' (0–20 m), 'Shelf' (20–200 m) and 'Deep' (slope and abyss, >200 m); the combination of both traits (substratum and water depth) gave rise to 24 general habitats as 24 divisions of the entire European marine sea floor. This approach based on habitat traits was preferred over field occurrence data for pragmatic reasons. Firstly, there is no large-scale and standardised survey that considers both macro- and megabenthos covering the large spectrum of water depths and substratum types; the current EUNIS marine habitat classification (Galparsoro et al. 2012), which is gaining recognition, does not provide species lists per habitat except a few iconic ones, and performs poorly when related to changes in community composition (Cooper et al. 2019). Secondly, the long history of bottom trawling on the European shelves has rendered this perspective unrealistic; at present, the sea floor is still swept by trawlers and in many places, can be abraded several times a year, and it has lost most of its historical large biogenic structures (de Groot 1984, Houziaux et al. 2011). Thus, our physical habitats were theoretically ideal, as they represent undisturbed conditions in which species may occur independently of their vulnerability. Using presence–absence is not necessarily worse than a more empirical context of field abundance data, as assembly rule control on communities is primarily exerted on species presence, especially at the large scale when differences between habitats are expected to be strong (Wilson 2012). In this way, data analyses can provide theoretical predictions on functional diversity patterns for the many European areas that have experienced long-lasting and continuous effects of human pressures and where species abundances may have been driven far from historical references.

2.1.3. Response traits

Response traits were used to test H_3. The traits considered were those defined by Beauchard et al. (2021), specifically scored and combined in a sensitivity component that expresses the instantaneous

effect of physical disturbance on a species, and a recoverability component that indicates the inability of this species to recover (Supplement 2). Although the sensitivity component was specifically designed for studying bottom trawling impact, the recoverability component, based on growth rate, reproductive ability and dispersal, is generic for any kind of disturbance. The sensitivity (SE) component was calculated as:

$$SE = BL \times FR \times BD \qquad (1)$$

where BL is body length, FR is body fragility, and BD is burrowing depth, used as effect traits ('Substratum depth distribution'); trait modalities are scored to express vulnerability (e.g. in the case of BD, the highest score is given to epibenthic species, and the lowest to deep-burrowing ones). As our trait approach provides an ideal undisturbed context where any vulnerable species can occur in its documented habitats, the recoverability component (RE) was calculated in a conservative way using only life span (LS) instead of the relative maturity ratio for intensively trawled areas:

$$RE = LS \times MO \times OT \times OS \qquad (2)$$

where MO is mobility (used to quantified sediment mixing types), OT is offspring type, and OS is offspring size.

2.2. Data analyses

2.2.1. Functional groups and species structural properties

The fuzzy coded species × effect traits matrix was processed using a multivariate ordination technique. In a typological perspective, our aim was to find correspondences between species and trait modalities as strong as possible so that the matrix was transformed by double-multiplicative centring (chi-squared metrics) as processed through fuzzy correspondence analysis (FCA; Chevenet et al. 1994). FCA axes maximise the sum of trait correlation ratios; for a trait, this ratio is the variance of modality scores divided by the axis variance (eigenvalue) and varies from 0 (no trait expression) to 1 (optimum). Usually, the application of FCA is sufficient for deriving species–modality correspondences and species groups. However, we also aimed at quantifying species functional niche breadth to assess species multifunctionality, so we used a more specific procedure. The 15 fuzzy traits, each with m modalities, are 15

multivariate measurements of each species and can be seen as 15 matrices of 812 species × m modalities, returning 15 clouds of species through 15 separate FCAs. As a simultaneous ordination, multiple factor analysis (MFA; Escofier & Pagès 1994, Abdi et al. 2013) was used to project these 15 clouds of species onto a unique system of multivariate axes (Fig. 2). MFA provides species-averaged axis scores of the 15 ordinations; correlation ratios were recalculated with species axis scores (unit norm, SD = 1) and the fuzzy
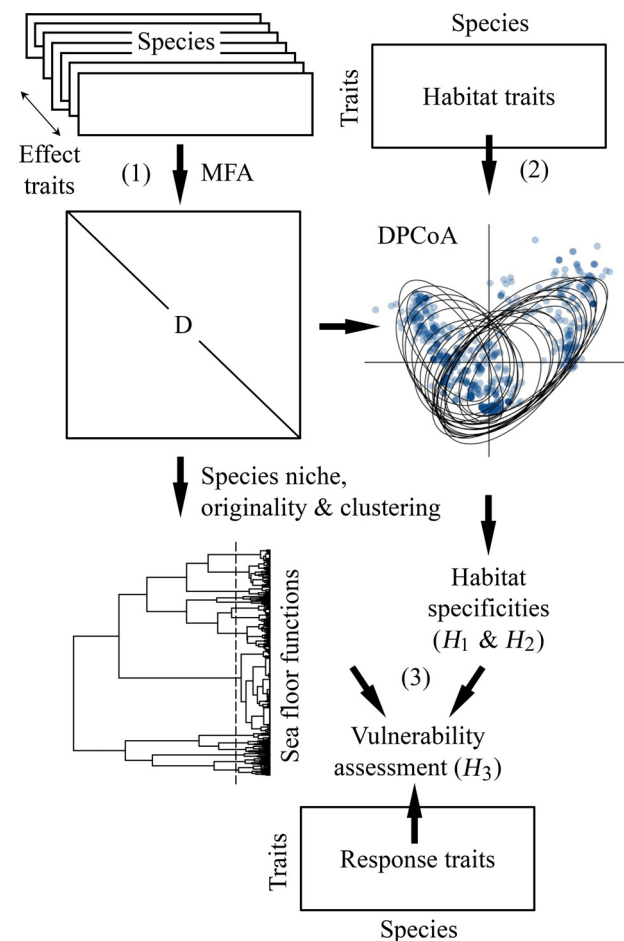

Fig. 2. Analytical approach. (1) 15 species × effect traits matrices are separately processed by 15 fuzzy correspondence analyses, and then simultaneously coordinated through multiple factor analysis (MFA); a Euclidean distance matrix (D) is derived from MFA species axis scores and used for computing species structural properties and clustering species as typological groups of sea floor functions. (2) The combination of matrix D with species × habitat traits through double principal coordinate analysis (DPCoA) enables to test H_1 (habitat–function relationships) and H_2 (habitat–functional diversity relationship). (3) The species × response traits matrix is used to distribute species vulnerability for each sea floor function on the one hand, and along the habitat gradient on the other hand, in order to test H_3 (no difference in vulnerability between functions)

coded data matrix (according to Chevenet et al. 1994). Hence, the niche breadth of a species can be expressed by the variance of its 15 axis scores along an MFA axis (sum of variances in the case of several axes). MFA is a multi-table ordination technique (Thioulouse et al. 2018) that better takes account of structural importance of column blocks (here, the traits) with weighting options specific to the research context. We chose the division of each matrix by its first eigenvalue from its respective FCA, which balances the roles of traits with different numbers of modalities (Escofier & Pages 1983). From the Euclidean distance matrix of the synthetic species MFA axis scores, we then also computed functional originality under 2 complementary versions from Pavoine et al. (2017). The first one, the Rb index, as the first eigenvector of this distance matrix, is an improved version of the averaged distance between species, and reveals how close species are to the most distant edges of the pattern. The second one, the NN index, is the distance to the nearest neighbour and expresses the degree of functional redundancy in the trait space. Sea floor species functional groups were simply derived from a hierarchical clustering based on Ward's aggregation criterion (Murtagh & Legendre 2014) applied to the Euclidean distances between average MFA species positions.

2.2.2. Habitat–function relationships

The distributions of sea floor functions among habitats were explored through double principal coordinate analysis (DPCoA; Pavoine et al. 2004). DPCoA positions habitats at the gravity centres of their respective species based on a habitat × species matrix constrained by a matrix of species functional distances; we used the Euclidean distances between species MFA axis positions that encompassed the main sea floor functional information. The resulting axes maximise the positions of habitats constrained by species functional distances, species being positioned by passive projection; hence, axes maximise β-functional diversity (i.e. between habitats). H_1 was tested by an appropriate procedure that randomly permutes species among habitats in order to consider whether habitats could be distinguished according to their functional contributions (Pavoine & Dolédec 2005); the procedure compares simulated γ-functional diversity values, the β- over α-habitat diversity ratio, to the observed one (999 permutations). Although very intuitive when comparing extreme habitats (i.e. hard vs. mud), H_1 was tested to support the correlative validity of the trait data as should be expected with field data (Pearson 2001): substratum type should at least differ in suitability to species functional types.

Concomitantly to DPCoA, we used Rao's quadratic entropy index (Rao 1982), an ultimate measure of α-functional diversity, the sum of weighted squared distances between species, as an average between-species distance within a habitat. This enabled us to test H_2, according to which soft sediment habitats were more functionally diversified. As shown by Mouchet et al. (2010), Rao's index is intermediate between convex hull (species community volume as functional range in the trait space) and functional divergence (how species tend to diverge from the community centroid). Thus, from this point of view, removing species from a community with a high Rao's index can substantially alter the functional potential of the community (Ricotta et al. 2016).

2.2.3. Vulnerability analysis

Sensitivity, recoverability and vulnerability, the latter as the combination of the first two, were compared between functional species groups and between habitats using non-parametric and correlative approaches.

All analyses and associated graphical representations were carried out using R 4.2.2 (R Core Team 2022). Multivariate analyses were processed with the package 'ade4' (Chessel et al. 2004), and functional originality with the package 'adiv' (Pavoine 2020). Group comparisons were done with a Kruskal-Wallis test, and, in case of significance (p < 0.05), we applied post hoc multiple comparisons of Dunn's test with the package 'dunn.test' (Dinno 2017), with Bonferroni adjustment of the p-values (0.025 as rejection level). Fig. 2 summarises our analytical methodology.

3. RESULTS

3.1. Species typological groups

MFA of the effect trait matrix revealed a complex pattern, spreading along 7 axes accounting for 48% of the total inertia (Fig. 3); Table 4 displays the correlation ratios of each trait on each axis. The first axis sharply opposed epibenthic species (left) to burrowing ones (right), and the second axis captured the vertical distribution across the substratum (Fig. 4b). Characteristic traits were covariant along this burrowing depth gradient (Fig. 4c–k). A few epi-bioconstructions were also characteristic of the
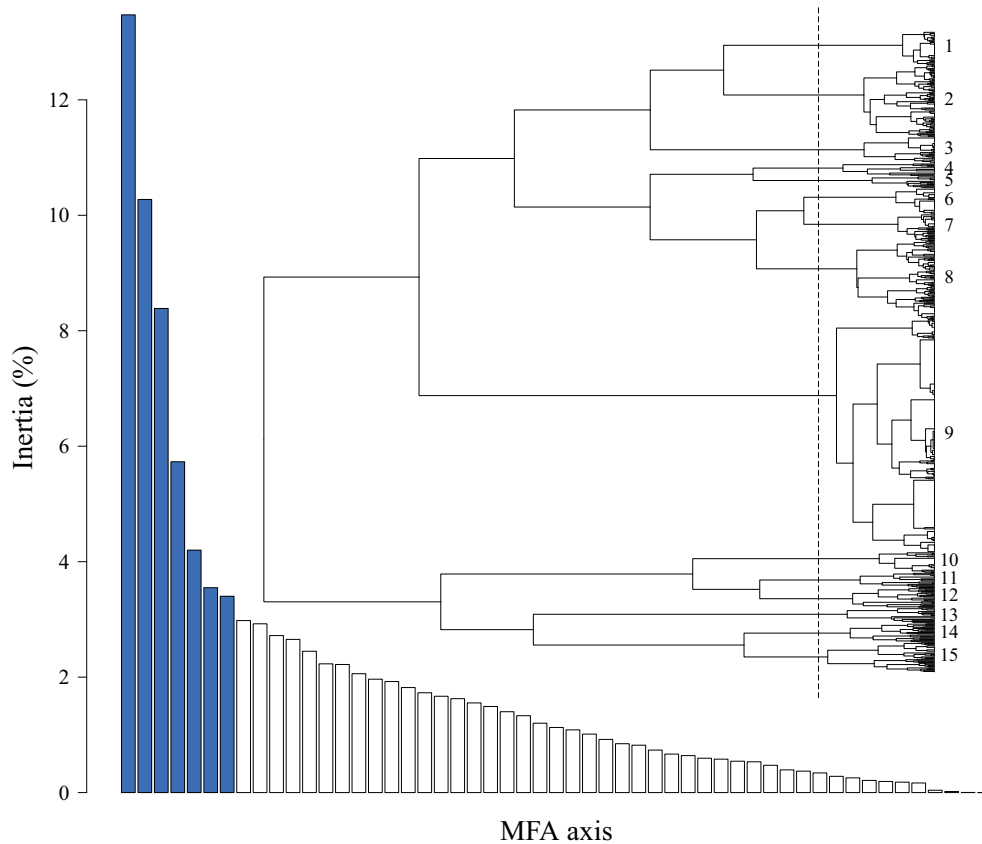
Fig. 3. Multiple factor analysis (MFA), eigenvalue diagram showing the 7 axes kept for interpretation (blue). Dendrogram, cluster analysis of Euclidean distances between species scores on the 7 selected axes; the optimal partition results in 15 groups of species

burrowing fauna (Fig. 4l–n), such as mounds (Fig. 4l) resulting from upward conveying (Fig. 4e). The third and fourth axes were mostly related to epi-bioconstruction and biodeposition (Fig. 5). Axis 5, 6 and 7 brought only limited variations regarding a few species groups, displayed in Supplement 3,

Figs. S3.1 & S3.2. Taxonomy poorly explained the pattern, except along axes 3 and 4 where phyla were more specific of epi-bioconstruction type and size (Fig. S3.3). We derived 15 typological species groups of sea floor functions from the cluster analysis (Fig. 3; Supplement 1); group composition is

Table 4. Correlation ratios of traits on each axis of the multiple factor analysis; only traits with substantial species discriminatory power (>0.20) are represented in Figs. 4 & 5

|	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7
Substratum depth distribution	0.38	0.29	0.05	0.12	0.07	0.04	0.04
Biodiffusion	0.00	0.32	0.16	0.09	0.00	0.25	0.00
Downward conveying	0.52	0.13	0.04	0.00	0.05	0.00	0.18
Upward conveying	0.23	0.38	0.10	0.07	0.10	0.01	0.10
Regeneration	0.01	0.22	0.01	0.06	0.10	0.00	0.08
Bioerosion	0.07	0.05	0.08	0.19	0.19	0.48	0.15
Biodeposition	0.08	0.18	0.46	0.02	0.25	0.06	0.06
Biostabilisation	0.42	0.19	0.01	0.01	0.02	0.02	0.01
Ventilation/Pumping	0.67	0.34	0.09	0.02	0.03	0.01	0.13
Endo-bioconstruction type	0.84	0.33	0.02	0.08	0.12	0.36	0.05
Endo-bioconstruction depth	0.81	0.45	0.07	0.09	0.19	0.06	0.13
Endo-bioconstruction width	0.81	0.35	0.17	0.00	0.09	0.05	0.09
Epi-bioconstruction type	0.54	0.62	0.86	0.70	0.32	0.09	0.28
Epi-bioconstruction extension	0.39	0.37	0.84	0.53	0.29	0.07	0.17
Epi-bioconstruction size	0.16	0.33	0.81	0.57	0.05	0.07	0.04
Inertia (%)	13	10	8	6	4	4	3
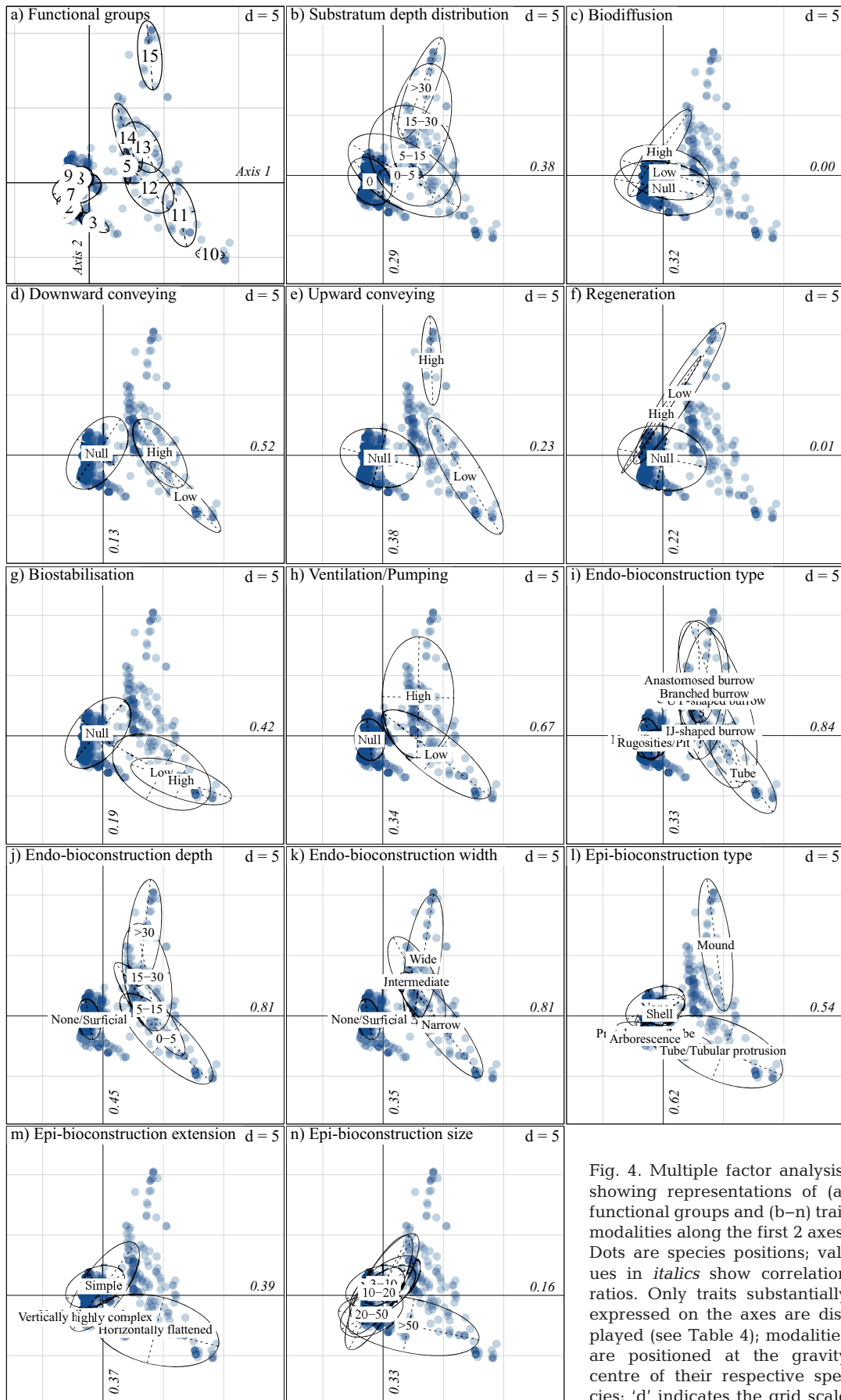
Fig. 4. Multiple factor analysis, showing representations of (a) functional groups and (b–n) trait modalities along the first 2 axes. Dots are species positions; values in *italics* show correlation ratios. Only traits substantially expressed on the axes are displayed (see Table 4); modalities are positioned at the gravity centre of their respective species; 'd' indicates the grid scale
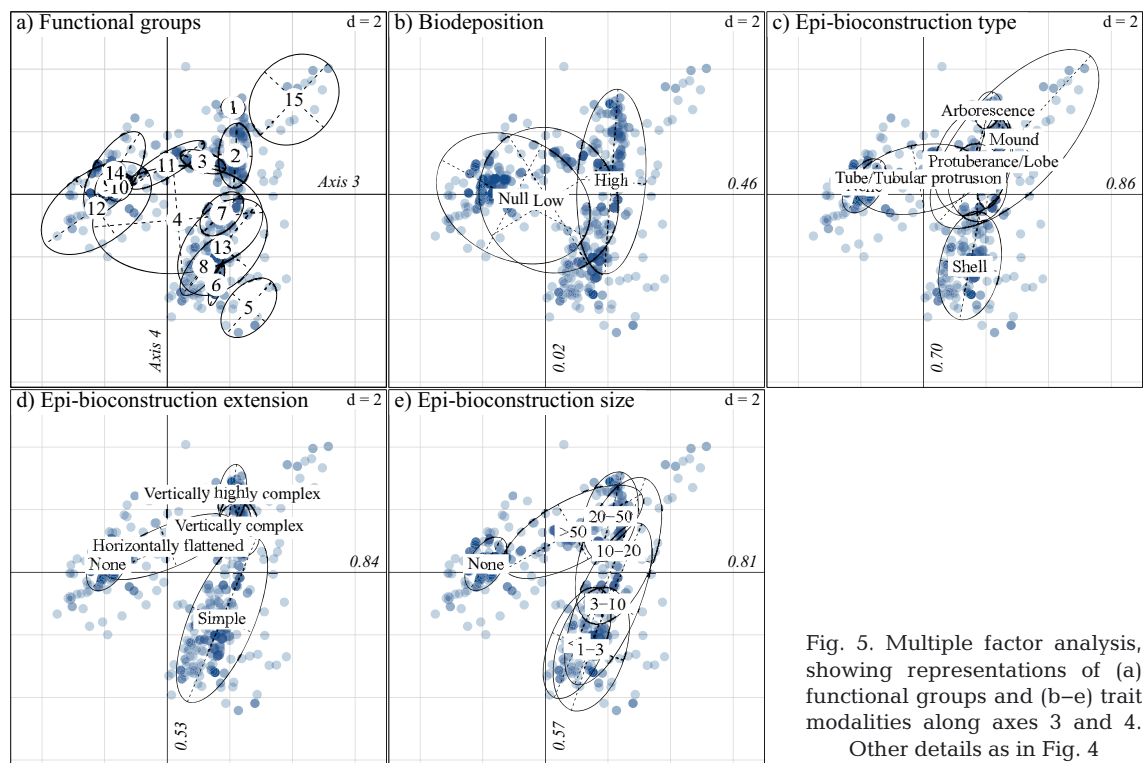
Fig. 5. Multiple factor analysis, showing representations of (a) functional groups and (b−e) trait modalities along axes 3 and 4. Other details as in Fig. 4

summarised in Table 5, with a detailed description provided in Supplement 4.

Burrowing groups exhibited broader functional niches (Fig. 6a), which means that species from these groups were characterised by more divergent trait modalities; Figs. S3.4−S3.7 illustrate this aspect on the MFA factorial planes. Functional originality expressed through the Rb index was closely related to niche breadth (r = 0.90, p < 0.001), indicating that species with divergent modalities (high Rb) had uncommon trait modality combinations (Fig. 6b) and were distributed at the edges of the species cloud (Figs. 4a & 5a). The NN index (functional originality, nearest neighbour) provided relatively independent information to Rb, as the two were not strongly correlated (r = 0.38, p < 0.001). Differences between groups were less obvious due to higher within-group variations, but slightly higher values were also found in burrowing groups (bioturbators). Among non-burrowing groups, epibenthic erect and bioeroding species had slightly broader niche breadths and Rb index values.

The MFA and species structural property patterns provided robust support for H_1 and H_2. MFA axes clearly displayed a duality between below- and above-substratum engineering. Aspects related to endo-bioconstructions dominated MFA axis variance

as they were necessarily associated with sediment mixing types that were covariant with burrow and tube creation, typical of soft sediments. This covariance was the main support of H_2, as these functionalities are more limited in hard substrata, whereas soft ones harbour various epi-bioconstructions including the most prominent ones like tube lawns, and also shellfish reefs that occur on hard substrata (Supplement 1). Moreover, below- and above-substratum engineering were not completely independent. Mound and tube building, associated with in-sediment processes such as bioturbation (e.g. upward or downward conveying), could largely account for the broader niche breadths in burrowing groups.

3.2. Habitat−function relationships

Significant differences in functional composition were detected between habitats (p < 0.001). The functional information accounted for 9% of habitat variation (i.e. of total inertia). The DPCoA pattern exhibited a clear habitat gradient from hard (left) to soft substrata (right; Fig. 7b). Rao's quadratic entropy (functional α-diversity) was strongly associated with this gradient (Fig. 7c; r = 0.89, p < 0.001). This result was not influenced by differences in species richness be-

Table 5. Summarised description of the functional groups and their habitat preferences. Under 'Abbreviation', values within parentheses indicate the number of species in the group. Habitats are H: hard; MH: mixed hard; G: gravel; S: sand; MS: muddy sand; M: sandy mud–mud; total numbers of species per substratum type are given in parentheses; values in rows are percentages of the number of species of the respective functional group. See Supplement 4 for detailed group descriptions

Group Code	Abbreviation	Description	Habitat preferences					
			H (370)	MH (338)	G (148)	S (280)	MS (278)	M (224)
1	EpiErect (42)	Epibenthic, tall and erect arborescence. Mostly corals and sponges.	53	34	3	4	3	4
2	EpiLarge (91)	Epibenthic, possibly erect, less complex. Large, isolated or through horizontal extensions (e.g. mussel reef, sea pen forest, sponge aggregation).	40	29	8	8	9	6
3	Fouler (34)	Epibenthic, fouling organisms forming mats (e.g. barnacles, serpulid worms).	40	35	6	6	8	6
4	MajAbr (16)	Major abrading effect on hard substrata (urchin or sponge).	48	32	6	3	6	3
5	Borer (15)	Boring into hard substrata, building burrows (typically bivalves).	44	21	9	9	9	9
6	MinAbr (33)	Minor abrading effect on hard substrata (typically gastropods).	56	31	4	7	2	0
7	EpiSmal (34)	Epibenthic, sessile, extended mat or isolated forms (e.g. solitary corals, sea squirts, hydrozoans).	46	37	6	3	5	3
8	ShalShel (99)	Mostly shallow-buried, shelled species (bivalve-dominated). Can occur above substratum (some gastropods).	8	10	15	25	26	16
9	SurfDiff (296)	Generally mobile, possibly buried (at least intermittently) Most generate surficial sediment diffusive mixing (various arthropods, molluscs and echinoderms).	17	21	11	23	15	13
10	SmallTub (26)	Small tubicolous worms, extensive mats in sediment or on rock with possible erosive ability (e.g. spionids).	7	3	10	20	32	27
11	DeepTub (19)	Deeper tubicolous worms (e.g. phoronids), larger with extensive tube mats (e.g. *Haploops* spp., *Lanice conchilega*) or burrow with mound mat (e.g. *Corophium* spp.).	6	9	6	18	30	30
12	MinBiot (25)	Minor bioturbators, mostly worms in narrow burrows.	10	14	10	10	29	27
13	SesBiot (24)	Sessile bioturbators, in deep vertical (e.g. *Mya* spp.) or shallow burrows with several openings (*Amphiura* spp.). Active bioirrigators.	0	3	5	19	38	35
14	MajBiot (38)	Major bioturbators, larger, mobile, with deep bioturbative effects (e.g. heart urchin, ragworm).	3	7	5	23	34	27
15	Deep 3D (20)	Deepest burrowers, bulldozing effect on the sediment with large galleries (typically callianissids, lobsters, lugworms).	0	3	0	14	41	41

tween habitats (Table 5), as no significant correlations were observed between species richness and DPCoA axis scores (axis 1, r = −0.22, p = 0.294; axis 2, r = 0.07, p = 0.734). Benthic functional diversity increased 3-fold from hard to soft substrata (Fig. 7c). Along this gradient, 3 main associations of functional groups could be distinguished (from left to right): hard–epibenthic, coarse sediment–surficial and shelled diffusors, mud-bioturbators and small tubes (Fig. 7d); group 5 (borers) occupy hard substrata, but these organisms can be found in all habitats where driftwood is cast. There was no clear depth trend, except within muddy habitats, stretched from top right (intertidal) to bottom middle (deep), and within hard habitats, stretched from bottom middle (intertidal) to top left (deep); see Fig. S3.8 for details.

Species niche breadth and Rb index were positively correlated with the first axis (r = 0.61 and 0.55, respectively, p < 0.001 for both), while this was less the case for the NN index (r = 0.40, p < 0.001). Traits were passively projected on both axes in order to appraise their respective contribution to β-diversity. Modalities of most traits were aggregated in 2 modes, discriminating hard (left) from soft substrata (right). A few traits were continuously spread along the gradient, mainly epibenthic aspects (Fig. 7m–o).
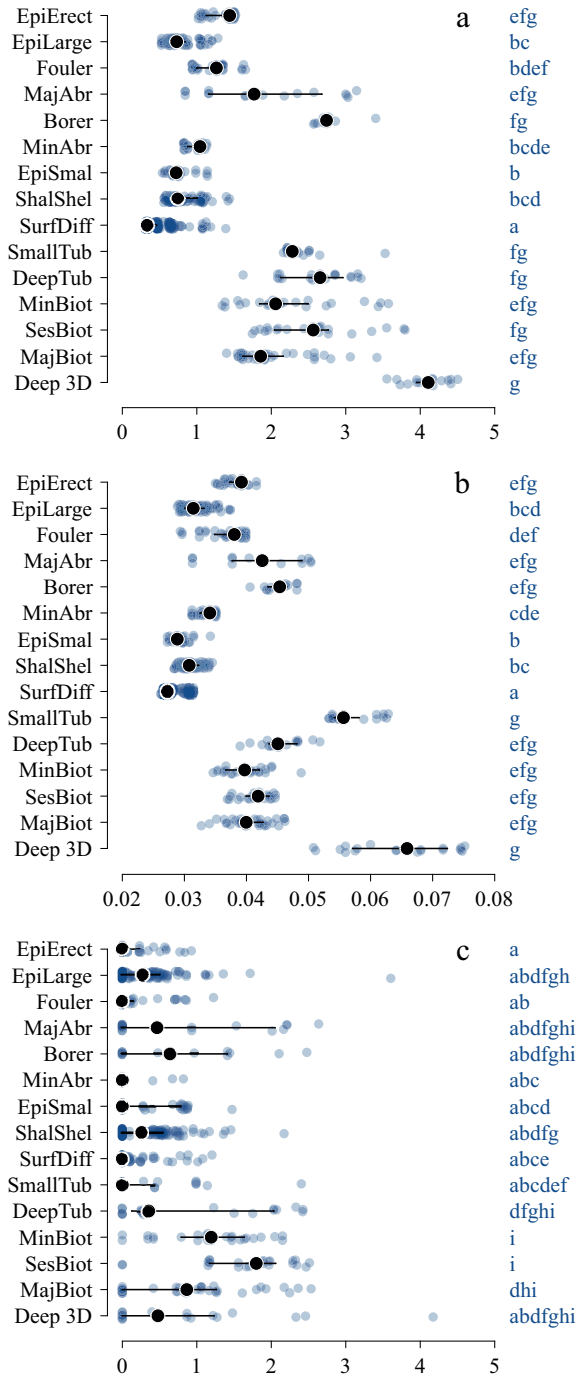
Fig. 6. Species structural properties per functional group derived from the trait space, i.e. multiple factor analysis (MFA) axes as displayed in Fig. 4. (a) Functional niche breadth, amount of functional potential (see also Figs. S3.4–S3.7). (b) Functional originality as the degree of rarity of trait modality combination. (c) Functional originality as distance from the nearest neighbour species in the trait space. Blue dots, species; black dots, median; bars range from 25th to 75th percentiles. Right side, the absence of common letters between 2 groups denotes a significant difference; Bonferroni-corrected significance level of Dunn's test, $p \leq \alpha/2$, i.e. 0.025. Group abbreviations as in Table 5
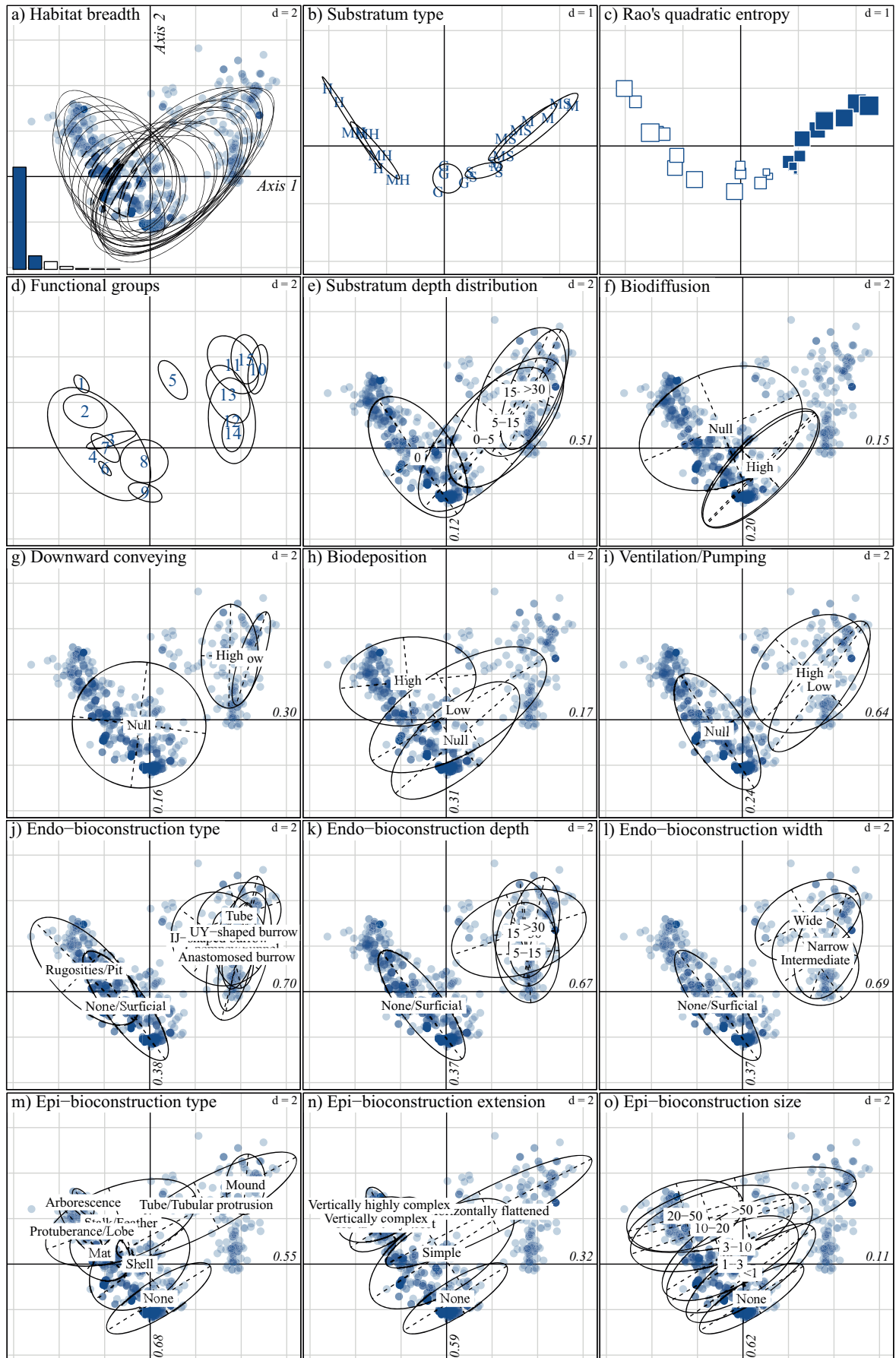
The second axis mostly opposed gravel and sand (bottom) to deep hard and shallow muddy habitats (top), with increasing biodeposition and epi-biocon-struction type and size (Fig. 7h,m–o); this axis em-phasised the similar importance of hard and muddy habitats in providing emergent structures. Stronger correlations with niche breadth and Rb index were found (r = 0.79 and 0.78, respectively; p < 0.001 for both), but not for NN index (r = 0.41, p < 0.001).

These results validate H_1 and H_2, and the relation-ships between the habitat gradient (first DPCoA axis) and species structural properties show higher spe-cies multi-functionality in soft substrata by diversifi-cation of epi-, endo-substratum engineering or both as detailed in the MFA pattern.

3.3. Sea floor function vulnerability

No major differences in sensitivity, recoverability and vulnerability were found between the sea floor functional groups and the habitats (Fig. 8). The dif-ferences of groups 1 and 2 (large epi- bioconstruc-tions) were slightly more perceptible, higher for the 3 indices. Fig. 8 displays the variations of the 3 indices along the first DPCoA axis that account for the habi-tat gradient, from hard (left) to muddy (right), and shows 3 similar trends. As a result of group 1 and 2 habitat specificity (Fig. 7d), sea floor function vulner-ability is mostly notable in deep hard substrata for the functions ensured by these groups (see Fig. S3.8 for depth gradient). This partly affected the validity of H_3, yet vulnerability remained weakly variable beyond these habitats along the gradient.

Fig. 7. Double principal coordinate analysis; each panel dis-plays the same multivariate axes along which species (blue dots), habitats, functional groups and trait modalities simi-larly positioned can be associated. (a) Habitat breadth, with ellipses encapsulating the respective species of each of the 24 habitats, illustrating α-functional diversity; bar diagram, eigenvalues; axis 1, 80 %; axis 2, 11 %. (b) Habitats grouped per sediment type (centroids of ellipses in a); H, HM, G, S, MS and M represent respectively hard, mixed hard, gravel, sand, muddy sand and sandy mud–mud; each character cor-responds to a specific depth; see Fig. S3.8. (c) Rao's index as α-functional diversity; white and blue squares (habitat posi-tions in b) for respectively low and high values; square size proportional to the deviation from the mean (small square); values range from 11.5 (min, left) to 31.5 (max, right). (d) Functional groups highlighted in the MFA (Figs. 3–5) and positioned according to species scores. (e–p) Traits exhibit-ing a substantial correlation ratio on the first or the second axis (values in *italics*), hence contributing to β-diversity. 'd' indicates the grid scale
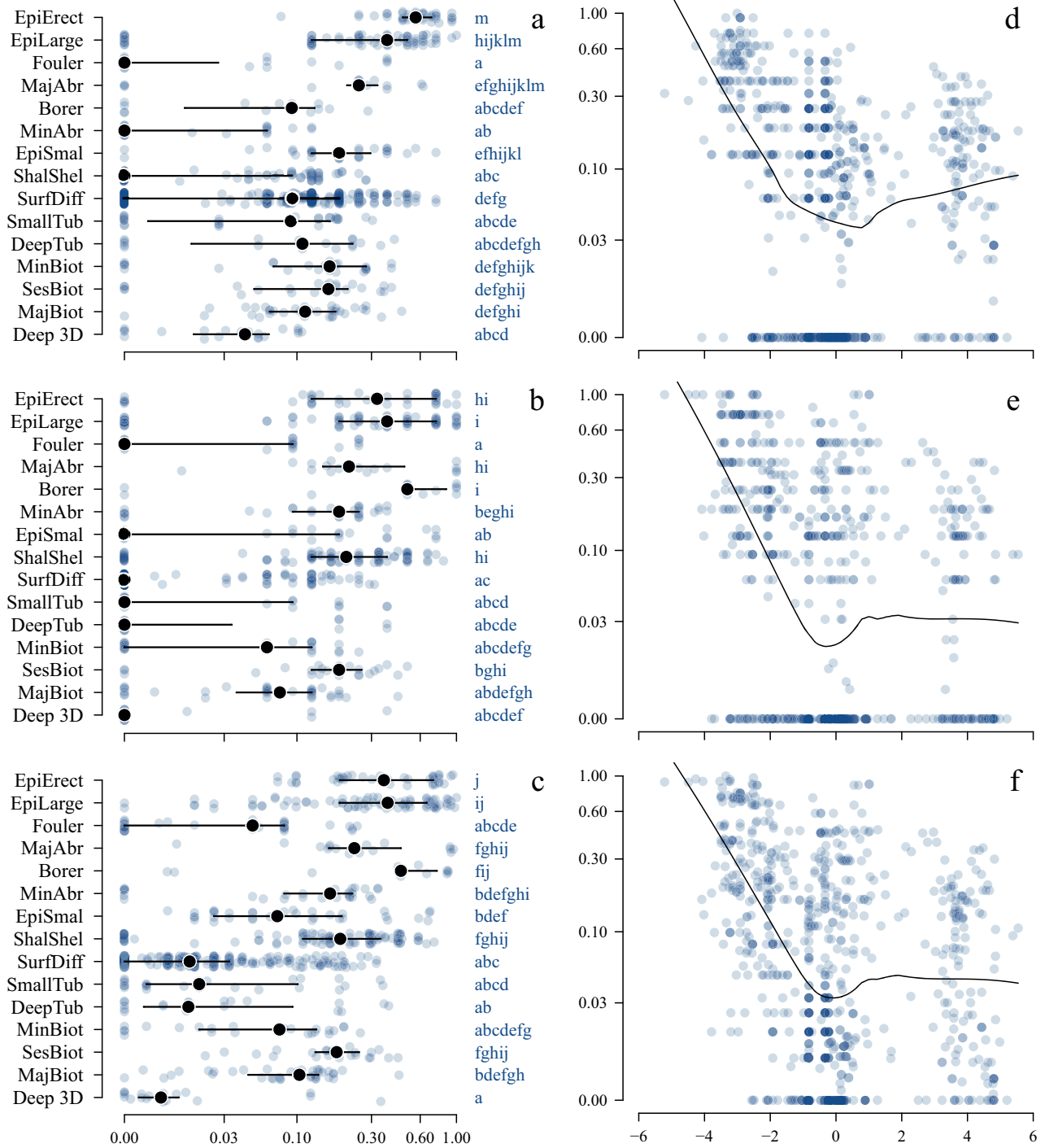
a) Habitat breadth

b) Substratum type

c) Rao's quadratic entropy

d) Functional groups

e) Substratum depth distribution

f) Biodiffusion

g) Downward conveying

h) Biodeposition

i) Ventilation/Pumping

j) Endo−bioconstruction type

k) Endo−bioconstruction depth

l) Endo−bioconstruction width

m) Epi−bioconstruction type

n) Epi−bioconstruction extension

o) Epi−bioconstruction size

Fig. 8. Vulnerability analysis. (a–c) Responsive characteristics of functional groups to disturbance; blue dots, species; black dots, medians; bars range from 25th to 75th percentiles. From a to c, *x*-axis: sensitivity (instantaneous response), recoverability (long-term response) and vulnerability (sum of sensitivity and recoverability). Right side, the absence of common letters between 2 groups denotes a significant difference; Bonferroni-corrected significance level of Dunn's test, p ≤ α/2, i.e. 0.025. (d–f) Corresponding variations in sensitivity, recoverability and vulnerability (vertically) along the first double principal coordinate analysis (DPCoA) axis (horizontally; axis 1 in Fig. 7a) as a habitat gradient, from hard (left) to muddy substrata (right); blue dots, species; black curve, non-parametric LOWESS fitting; the 3 variations are similarly due to species from groups 'EpiErect' and 'EpiLarge' (large epibenthic and slow-growing species) in deep, hard substrata, beyond which no variation is observed

4. DISCUSSION

4.1. Effect traits and functional groups

Although we derived interesting outcomes from our effect trait data set, some words of caution are warranted. In a local context, on a more limited set of species, the use of these traits might have some limitations. As displayed in Fig. 7, burrowing and bioturbative aspects can denote a lack of habitat specificity, especially from sand to mud. In case of limited sedimentary variations, the traits may fail in identifying habitat-specific functions or engineering effects on community composition. As Murray et al. (2014) reported, this may prevent translation into accurately and quantified sediment mixing rates and solute fluxes that require a high level of detail regarding the involved species. Although our set of traits was more comprehensive and finely designed than existing data sets (e.g. Queirós et al. 2013), their use was more intended from the perspective of functional potential and diversity assessment rather than quantitative nutrient budgets. For instance, sedimentary mounds, which simultaneously ensure habitat, biogeochemical and physical functions, typically fall within this perspective.

The functional groups were relatively specific to substratum depth distribution, although the deeper they reach, the larger the depth interval becomes (Fig. 4b). This could be expected given the more demanding respiratory requirements in deeper sediments (Kristensen & Kostka 2005) and habitat depth-specificity of sediment mixing (Pearson & Rosenberg 1978, Pearson 2001). Among different functions that species could ensure regardless of their burrowing depth, there was no exclusive association between the different species groups and the traditionally considered dichotomy in ecosystem engineering, i.e. autogeny versus allogeny. While large epi-bioconstructions are known to create habitats (e.g. biogenic reefs, i.e. autogeny), they can also maintain substantial fluxes of matter from the water column to the sea floor (biodeposition, i.e. allogeny). Some species from group 1 and 2 (large epibenthic forms) certainly display more of an autogenic than an allogenic character (e.g. *Desmophyllum pertusum*; Howell et al. 2011), but many tube dwellers display both equally, like the prominent sediment accretions created by patchy lawns of *Lanice conchilega* (Rabaut et al. 2009, Braeckman et al. 2010). To capture such terminological issues, also for other biological descriptors, we think that a fuzzy concept is more suitable than a simplistic dichotomic one. In this respect, the impli-

cation of functional niche breadth, expressing multi-functionality, is determinant, as discussed below.

4.2. Implications of functional niche and originality

The validation of H_1 and H_2 was greatly supported by our trait analyses. We could have concluded that the increase in functional diversity toward soft sediment habitats would have solely resulted from an increase in functional dissimilarity between species as expressed by Rao's index. In fact, larger niche breadths encountered in soft sediment species provide additional evidence: although species can dwell above or below sediment surface, they can engineer both compartments. The DPCoA pattern clearly showed the contribution of bioturbation to this increase, but other above-substratum engineering also contributed. The multi-functional importance of soft sediment benthos, although first developed >20 yr ago (Snelgrove 1999, Snelgrove et al. 2014), had never been made explicit with tangible quantifications until now.

Species of broader functional niche breadth were also those of greater functional originality expressed by the Rb index. In general, an increase in functional diversity is due to functional niche differentiation (Ricotta et al. 2016), and rarity in trait combinations exacerbates dissimilarity (Kondratyeva et al. 2019). This is exemplified by historical evidence in the marine benthos, where the functional diversity increased over evolutionary time due to emerging species with rare trait combinations (Villéger et al. 2011). However, we cannot ascertain a direct link between originality and niche breadth, although both were strongly correlated. In any case, the functional niches of species from different soft substratum groups can largely overlap (Figs. S3.4 & S3.5) in spite of dissimilar niche centroids (Fig. 4a) and similar habitat occupancy (Fig. 7d). Such niche overlap may not necessarily preclude species from coexisting, as niches derived from effect traits do not necessarily reflect Hutchinsonian niches derived from response traits, of which overlap can lead to competitive exclusion (see Section 1).

Given the paucity of marine studies using functional originality, some technical remarks deserve discussion in light of our results. The Rb index better discriminated the functional groups than the NN index, both being weakly correlated. The NN index is a special case of originality, expressing uniqueness (Pavoine et al. 2017); it equals 0 in species sharing the same functional niche, and increases with niche iso-

lation in the functional space. In our context, the large biogeographic species pool necessarily contains sister species with similar niches but differing in geographic distribution, leading to large variations in the NN index within functional groups. For instance, the largest discrepancy between Rb and NN indices was encountered in group 15, with the highest Rb index, which includes all mud shrimps recognised for their important role in ecosystem functioning (Atkinson & Taylor 2005): *Calocarides coronatus*, *Calocaris macandreae*, *Callinassa subterranea*, *Gilvossius tyrrhenus*, *Jaxea nocturna*, *Necallianassa truncata* and *Upogebia* spp. These species, which have a similar functional niche, are commonly encountered from the northwest shelf to the Mediterranean Sea, but can locally be represented by only 1 species. Thus, whereas their NN scores ranged between 0 and the median score of the entire species pool (Table S1.1), they may get a maximum uniqueness in local studies when a single one of these species is represented. More generally, high Rb and NN indices characterise low functional redundancy (Pavoine et al. 2017), so species of high originality are irreplaceable. This represents a critical point as regards management implications: in the case of the mud shrimps previously mentioned, which exhibit broad niche breadths, their rarefaction should attract particular attention.

4.3. Vulnerability assessment

The high number of significant functional gradients returned by MFA (7) may reflect a multiplicity of engineering types within a few life strategies. Among multiple examples, long-lived and slow-growing species (i.e. *K*-strategists) are encountered under very diverse engineering modes: reef building by Pacific oyster *Magallana gigas*, crawling on the sediment by red king crab *Paralithodes camtchaticus* or burying below the water–sediment interface by the North Atlantic quahog *Arctica islandica*. Similarly, short-lived species (e.g. *r*-strategists) have developed contrasting structures and functions, like tube lawns of the sand mason worm *L. conchilega*, deep anastomosed galleries of mud shrimps *C. subterranea* or foliaceous erect forms of the hornwrack *Flustra foliacea*. Many of these dwelling forms can be indistinctly found in species of low or high recoverability following anthropogenic impacts. To a lesser extent, large epi-bioconstructors, very exposed to abrasive forces and requiring a long time to achieve engineering after slow growth, seem to make an exception ('EpiErect' and 'EpiLarge'; Fig. 8a–c). This

mostly accounts for deep habitats where longer life spans are due to lower frequency of disturbance (Montero-Serra et al. 2018). Nevertheless, the outcomes from this work support the relative independence already suggested between fitness and engineering (Lavorel & Garnier 2002), at least in other habitats, as shown by the high variations in vulnerability to disturbance within most sea floor functions. Fig. S3.9 provides further evidence of the independence between response traits and sea floor functions, and shows that there is no obvious indication of mechanistic causality between life history and ecosystem engineering. Among species, a pending question concerns the rare trait combinations giving rise to broader functional niches in groups from muddy substrata. Disproportionate consequences of species removal for ecosystem functioning are questionable compared to hard substratum habitats, especially when species are present in low abundance (Leitão et al. 2016).

As expected, vulnerability was strongly variable within functional groups, likely due to the large number of species covering a wide biogeographic spectrum of ecosystem functions and life history strategies. Fig. 8 shows that from the perspective of conserving seafloor ecosystem functioning, no *a priori* priority should be given to any function or habitat. Large overlaps between functional group sensitivity, recoverability and vulnerability (Fig. 8a–c) suggest that various degrees of community vulnerability may be found at smaller scales where relative proportions in species community composition can strongly vary. Whereas an absence of overlap would have enabled us to address management priorities in habitats hosting vulnerable functions, local field expertise must be required to evidence differences in functional vulnerability. Whatever the expectations from local field studies, this opens the question of minimum regional surface area ensuring that all functions be protected, since functional diversity can be a growing function of space ('functional diversity area relationship', Smith et al. 2013).

Only a limited amount of sea floor functions can be encountered in a very limited surface area for several reasons. Firstly, as an inherent property of ecosystem engineering, one function can have inhibiting effects on another at the patch scale (Bouma et al. 2009, Norkko et al. 2006, van Wesenbeeck et al. 2007). Secondly, as supported by the validation of our first hypothesis, sea floor functions can be habitat-dependent as theoretically assumed or shown in studies carried out at various spatial scales (Hewitt et al. 2008, Bernard et al. 2019, Gogina et al. 2020). Fur-

thermore, ecosystem engineering can have positive effects on species richness over increasing spatial scales (Jones et al. 1997). This indicates that habitats are not interchangeable in terms of functions, but rather that seascape-scale protection may offer the greatest benefits by conserving the most functions provided by the benthos. Additionally, we are still unable to rank the highlighted sea floor functions in an order of importance for the ecosystem. Marginally, it could be said that the group of surficial diffusers (group 9) realises much less than other deeper burrowing groups so that gravelly and sandy habitats would contribute less than hard and muddy ones to ecosystem functioning as mentioned in other studies (Kenchington et al. 2001, Bolam et al. 2017). Moreover, in such more permeable sediments, bioturbation is reduced since fluxes are more abiotically induced (Meysman et al. 2006a, Timmermann et al. 2006). Also, we could speculate on the limited role of the fauna in deep muddy environments. Depth gradients were found in muddy habitats with a progressive impoverishment in burrowing structures and a preference for the sediment surface, as highlighted in the DPCoA pattern (Fig. S3.8), probably explained by lower oxygen concentrations and recognised depletion in burrowing fauna (Levin 2003); nevertheless, these habitats remain crucial for abiotic carbon burial (Middelburg 2018).

Should we preserve some sea floor functions at the expense of others under growing human pressures? Complementarity of functions over space is recognised (Godbold et al. 2011), so the impairment of one function may indirectly alter another one. For instance, coastal oyster reefs, as nursery grounds, and found on various substrata, can contribute to the survival of more widely distributed fish populations (Gilby et al. 2018). In fact, for most functions, we can only speculate on variable degrees of their local contributions to the functioning of the regional ecosystem. Hence, implementing protective measures requires multi-scale expertise and is further complicated by spatial contingencies. In general, the validity of the results displayed in Fig. 7 should increase with increasing extent of the area considered for protection due to an improved applicability of species and function−area relationships.

4.4. Fundamental and comparative considerations of benthic functional diversity

Our diversity analysis revealed higher functional potential in soft sediments than in hard substratum habitats, but it may be biased toward soft sediments, as the set of traits dominantly represents functions found uniquely in soft sediments (e.g. bioturbation traits). Although the existence of more complex biogeochemical processes in sediments is a reality (Snelgrove 1999, Snelgrove et al. 2018), it is worth comparing functional diversity solely based on epibenthic functionalities. When using only epibenthic traits, hard substratum habitats exhibit higher diversity from shore to deep (Fig. S3.10). Nevertheless, potential epibenthic functional diversity in soft sediments remains relatively high: whereas its maximum is 3-fold the minimum found in hard substrata when derived from all traits, the maximum found in hard substrata is barely 2-fold the minimum found in soft sediments when derived from epibenthic traits.

Furthermore, our analyses strengthen the importance of some comparative considerations on response and effect traits in assessing functional diversity. The response−effect trait framework has raised a growing debate about the use of functional traits, whereas there have been only few empirical attempts to tackle long-standing questions related to biodiversity and ecosystem vulnerability (de Bello et al. 2021, Oliver et al. 2015). The proper use of response traits ultimately leads to a limited number of life strategies as evolutionary convergences of trait modalities due to unavoidable trade-offs of energetic allocation in the 3 fitness components. This has been largely accepted in the general ecology literature, with a recent demonstration in marine benthic ecology supported by field data (Beauchard et al. 2022). The outcomes of our study support the fact that ecosystem engineering can result in fundamentally different diversity patterns compared to fitness. Trade-offs of energetic allocation limit the diversification of life strategies as evidenced by the existence of life history invariants (Charnov 1993). On the contrary, no evolutionary mechanism seems to rule marine benthic ecosystem engineering in the current state of knowledge, and the question of an equivalent of life history invariants for ecosystem engineering seems elusive. Rather than 3 or 4 functional groups as generally encountered in life strategies (Southwood 1988, Kindsvater et al. 2016), we highlighted 15 different groups consisting of species encompassing quite contrasting sea floor functions (at least 6−9 major extremities appear; Figs. 3−5). In the absence of a predictive mechanism, we could not expect fewer or more groups, but benthic functional diversity based on effect traits and in light of our results seems to be considerably greater than based on response traits.

4.5. Conclusions

The effect trait data set presented in this study offers interesting large-scale research opportunities in benthic ecology as shown by analytical support for key hypotheses related to ecosystem functioning. We must underline the usefulness of trait information at the species level, such as functional niche and originality, that bring mechanistic understanding of functional diversity patterns. Our exploratory analyses provided outcomes that, although supported at the biogeographic scale, might not be general at the local scale. Indeed, local species composition and relative abundances can be determined by environmental filtering (Beauchard et al. 2022). As we have shown, benthic ecosystem engineering can also depend on environmental conditions such as substratum, so local specific ecosystem engineering may correspond to specific life strategies, with consequently more specific sea floor function vulnerability. This advocates for empirical studies based on these effect traits and combined with field data along various habitat gradients in order to draw on what is general or context-dependent in benthic ecosystem engineering patterns. At least, our data, hypotheses and methodology offer directions for future empirical research in European waters.

Although the potentially higher soft substratum functional diversity found in this study may not always apply due to local exceptions, this outcome strongly emphasises the potential importance of soft sediment habitats in the marine ecosystem when compared to rocky habitats and their more charismatic species. As already stressed (Jones 1992, Jennings & Kaiser 1998, Houziaux et al. 2011, Steadman et al. 2021), the worldwide soft sediment shelf and slope ecosystems, that can be wrongly considered as flat, deprived of emergent structures and invariant, are experiencing a long-running devastation, especially through bottom trawling, while we are not able to completely address the question of historical ecosystem functioning. Current large-scale benthic impact or health status assessments (Eigaard et al. 2017, Mazor et al. 2021), which do not consider historical benthic state and are biased toward infauna, certainly do not account for large epibenthic species that are key drivers of functional diversity expansion in soft substrata, and may only reveal the tip of the iceberg. Our vulnerability assessment was insightful, as species vulnerability may not necessarily reflect vulnerability of ecosystem functioning. Consequently, protecting only species of low recoverability may not necessarily preserve the integral function-

ing, as many fast-recovering communities of high functional importance may be found in areas already heavily trawled. In addition to biodiversity conservation, the increasing concern about ecosystem capacity to supply services requires not only a focus on benthic organisms, but also on their short- and long-term effects on ecosystem functioning. In European waters, sea floor functions are expected to sustainably supply services (European Community 2008: Descriptor D6 of the Marine Strategy Framework Directive), but how best to conserve or to what extent this may be compromised by existing or future activities clearly requires further work.

LITERATURE CITED

Abdi H, Williams LJ, Valentin D (2013) Multiple factor analysis: principal component analysis for multitable and multiblock data sets. Wiley Interdiscip Rev Comput Stat 5:149–179

Atkinson RJA, Taylor ACA (2005) Aspects of the physiology, biology and ecology of thalassinidean shrimps in relation to their burrow environment. Oceanogr Mar Biol Annu Rev 43:173–210

Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanogr Mar Biol Annu Rev 44:123–195

Beauchard O, Veríssimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol Indic 76:81–96

Beauchard O, Brind'Amour A, Schratzberger M, Laffargue P, Hintzen NT, Somerfield PJ, Piet G (2021) A generic approach to develop a trait-based indicator of trawling-induced disturbance. Mar Ecol Prog Ser 675:35–52

Beauchard O, Mestdagh S, Koop L, Ysebaert T, Herman PMJ (2022) Benthic synecology in a soft sediment shelf: habitat contrasts and assembly rules of life strategies. Mar Ecol Prog Ser 682:31–50

Bernard G, Gammal J, Järnström M, Norkko J, Norkko A (2019) Quantifying bioturbation across coastal seascapes: Habitat characteristics modify effects of macrofaunal communities. J Sea Res 152:101766

Bodil BA, Ambrose WG, Bergmann M, Clough LM, Gebruk AV, Hasemann C, Włodarska-Kowalczuk M (2011) Diversity of the arctic deep-sea benthos. Mar Biodivers 41:87–107

Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages

between unimpacted habitats. Mar Environ Res 126: 1−13

Bouma TJ, Olenin S, Reise K, Ysebaert T (2009) Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgol Mar Res 63:95−106

Braeckman U, Provoost P, Gribsholt B, Van Gansbeke D and others (2010) Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. Mar Ecol Prog Ser 399:173−186

Callaway R (2006) Tube worms promote community change. Mar Ecol Prog Ser 308:49−60

Charnov EL (1993) Life history invariants. Some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford

Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package - I - One-table methods. R News 4:5−10

Chevenet F, Dolédec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. Freshw Biol 31:295−309

Coll M, Piroddi C, Steenbeek J, Kaschner K and others (2010) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLOS ONE 5:e11842

Cooper KM, Bolam SG, Downie AL, Barry J (2019) Biological-based habitat classification approaches promote cost-efficient monitoring: an example using seabed assemblages. J Appl Ecol 56:1085−1098

Dawkins R (1982) The extended phenotype. Oxford University Press, New York, NY

de Bello F, Lavorel S, Hallett LM, Valencia E and others (2021) Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. Trends Ecol Evol 36: 822−836

de Groot SJ (1984) The impact of bottom trawling on benthic fauna of the North Sea. Ocean Coast Manag 9:177−190

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646−655

Díaz S, Purvis A, Cornelissen JHC, Mace GM and others (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecol Evol 3:2958−2975

Dinno A (2017) dunn.test: Dunn's test of multiple comparisons using rank sums. https://CRAN.R-project.org/web/packages/dunn.test/index.html

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L and others (2017) The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES J Mar Sci 74:847−865

Escofier B, Pages J (1983) Méthode pour l'analyse de plusieurs groupes de variables. Application à la caractérisation des vins rouges du Val de Loire. Rev Stat Appl 31:43−59

Escofier B, Pagès J (1994) Multiple factor analysis (AFMULT package). Comput Stat Data Anal 18:121−140

Etter RJ, Mullineaux LS (2001) Deep-sea communities. In: Bertness SD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, MA, p 367−394

European Community (2008) Marine Strategy Framework Directive. 2008/56/EC EU. Off J Eur Union 164:19−40

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193−284

Galparsoro I, Connor DW, Borja Á, Aish A, and others (2012) Using EUNIS habitat classification for benthic mapping in European seas: present concerns and future needs. Mar Pollut Bull 64:2630−2638

Gérino M, Stora G, François-Carcaillet F, Gilbert F and others (2003) Macro-invertebrate functional groups in freshwater and marine sediments: a common mechanistic classification. Vie Milieu 53:221−231

Gilby BL, Olds AD, Peterson CH, Connolly RM and others (2018) Maximizing the benefits of oyster reef restoration for finfish and their fisheries. Fish Fish 19:931−947

Godbold JA, Bulling MT, Solan M (2011) Habitat structure mediates biodiversity effects on ecosystem properties. Proc R Soc B 278:2510−2518

Gogina M, Zettler ML, Vanaverbeke J, Dannheim J and others (2020) Interregional comparison of benthic ecosystem functioning: community bioturbation potential in four regions along the NE Atlantic shelf. Ecol Indic 110: 105945

Grime JP, Pierce S (2012) The evolutionary strategies that shape ecosystems. Wiley-Blackwell, Chichester

Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:79−90

Hewitt JE, Thrush SF, Dayton PD (2008) Habitat variation, species diversity and ecological functioning in a marine system. J Exp Mar Biol Ecol 366:116−122

Houziaux JS, Fettweis M, Francken F, Van Lancker V (2011) Historic (1900) seafloor composition in the Belgian–Dutch part of the North Sea: a reconstruction based on calibrated visual sediment descriptions. Cont Shelf Res 31:1043−1056

Howell KL, Holt R, Endrino IP, Stewart H (2011) When the species is also a habitat: comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it forms. Biol Conserv 144:2656−2665

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symp Quant Biol 22:415−427

Ingrosso G, Abbiati M, Badalamenti F, Bavestrello G and others (2018) Mediterranean bioconstructions along the Italian coast. Adv Mar Biol 79:61−136

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:201−352

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373−386

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946−1957

Jones JB (1992) Environmental impact of trawling on the seabed: a review. NZ J Mar Freshw Res 26:59−67

Kenchington EL, Prena J, Gilkinson KD, Gordon DC Jr and others (2001) Effects of experimental otter trawling on the macrofauna of a sandy bottom ecosystem on the Grand Banks of Newfoundland. Can J Fish Aquat Sci 58: 1043−1057

Kindsvater HK, Mangel M, Reynolds JD, Dulvy NK (2016) Ten principles from evolutionary ecology essential for effective marine conservation. Ecol Evol 6:2125−2138

Kondratyeva A, Grandcolas P, Pavoine S (2019) Reconciling the concepts and measures of diversity, rarity and originality in ecology and evolution. Biol Rev Camb Philos Soc 94:1317−1337

Kristensen E, Kostka JE (2005) Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. Coast Estuar Stud 60:125−157

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar Ecol Prog Ser 446:285−302

Lackschewitz D, Reise K (1998) Macrofauna on flood delta shoals in the Wadden Sea with an underground association between the lugworm *Arenicola marina* and the amphipod *Urothoe poseidonis*. Helgol Meeresunters 52: 147–158

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545–556

Leitão RP, Zuanon J, Villéger S, Williams SE and others (2016) Rare species contribute disproportionately to the functional structure of species assemblages. Proc R Soc B 283:20160084

Levin LA (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr Mar Biol Annu Rev 41:1–45

Matthews B, De Meester L, Jones CG, Ibelings BW and others (2014) Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. Ecol Monogr 84:245–263

Mazor T, Pitcher CR, Rochester W, Kaiser MJ and others (2021) Trawl fishing impacts on the status of seabed fauna in diverse regions of the globe. Fish Fish 22: 72–86

Meysman FJR, Galaktionov OS, Gribsholt B, Middelburg JJ (2006a) Bio-irrigation in permeable sediments: an assessment of model complexity. J Mar Res 64:589–627

Meysman FJR, Middelburg JJ, Heip CHR (2006b) Bioturbation: a fresh look at Darwin's last idea. Trends Ecol Evol 21:688–695

Middelburg JJ (2018) Reviews and syntheses: to the bottom of carbon at the seafloor. Biogeosciences 15:413–427

Montero-Serra I, Linares C, Doak DF, Ledoux JB, Garrabou J (2018) Strong linkages between depth, longevity and demographic stability across marine sessile species. Proc R Soc B 285:20172688

Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct Ecol 24:867–876

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28: 167–177

Murray F, Douglas A, Solan M (2014) Species that share traits do not necessarily form distinct and universally applicable functional effect groups. Mar Ecol Prog Ser 516:23–34

Murtagh F, Legendre P (2014) Ward's hierarchical agglomerative clustering method: Which algorithms implement Ward's criterion? J Classif 31:274–295

Narayanaswamy BE, Renaud PE, Duineveld GCA, Berge J, Lavaleye MSS, Reiss H, Brattegard T (2010) Biodiversity trends along the western European margin. PLOS ONE 5:e14295

Norkko A, Hewitt JE, Thrush SF, Funnell GA (2006) Conditional outcomes of facilitation by a habitat-modifying subtidal bivalve. Ecology 87:226–234

Odling-Smee J, Erwin DH, Palkovacs EP, Feldman MW, Laland KN (2013) Niche construction theory: a practical guide for ecologists. Q Rev Biol 88:4–28

Ólafsson E (ed) (2017) Marine macrophytes as foundation species. CRC Press, Boca Raton, FL

Oliver TH, Heard MS, Isaac NJB, Roy DB, Procter D, Eigenbrod F, Bullock JM (2015) Biodiversity and resilience of ecosystem functions. Trends Ecol Evol 30:673–684

Pavoine S (2020) adiv: an R package to analyse biodiversity in ecology. Methods Ecol Evol 11:1106–1112

Pavoine S, Dolédec S (2005) The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. Environ Ecol Stat 12:125–138

Pavoine S, Ricotta C (2021) On the relationships between rarity, uniqueness, distinctiveness, originality and functional/phylogenetic diversity. Biol Conserv 263:109356

Pavoine S, Dufour AB, Chessel D (2004) From dissimilarities among species to dissimilarities among communities: a double principal coordinate analysis. J Theor Biol 228: 523–537

Pavoine S, Bonsall MB, Dupaix A, Jacob U, Ricotta C (2017) From phylogenetic to functional originality: guide through indices and new developments. Ecol Indic 82:196–205

Pearson TH (2001) Functional group ecology in soft-sediment marine benthos: the role of bioturbation. Oceanogr Mar Biol Annu Rev 39:233–267

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229–311

Pickett STA, Kolasa J, Jones CG (1994) Ecological understanding: the nature of theory and the theory of nature, 2nd edn. Elsevier, Amsterdam

Queirós AM, Birchenough SNR, Bremner J, Godbold JA and others (2013) A bioturbation classification of European marine infaunal invertebrates. Ecol Evol 3:3958–3985

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rabaut M, Vincx M, Degraer S (2009) Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. Helgol Mar Res 63:37–46

Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. Theor Popul Biol 21:24–43

Ricotta C, de Bello F, Moretti M, Caccianiga M, Cerabolini BEL, Pavoine S (2016) Measuring the functional redundancy of biological communities: a quantitative guide. Methods Ecol Evol 7:1386–1395

Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. Ecol Appl 28:1302–1312

Rosenfeld JS (2002) Functional redundancy in ecology and conservation. Oikos 98:156–162

Rossi S, Bramanti L, Gori A, Orejas C (eds) (2017) Animal forests of the world: an overview. Marine animal forests. Springer, Cham

Schmera D, Heino J, Podani J, Erős T, Dolédec S (2016) Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. Hydrobiologia 787:27–44

Smith AB, Sandel B, Kraft NJB, Carey S (2013) Characterizing scale-dependent community assembly using the functional-diversity–area relationship. Ecology 94: 2392–2402

Snelgrove PVR (1999) Getting to the bottom of marine biodiversity: sedimentary habitats. BioScience 49:129–138

Snelgrove PVR, Butman CA (1994) Animal–sediment relationships revisited: cause versus effect. Oceanogr Mar Biol Annu Rev 32:111–177

Snelgrove PVR, Thrush SF, Wall DH, Norkko A (2014) Real world biodiversity–ecosystem functioning: a seafloor perspective. Trends Ecol Evol 29:398–405

Snelgrove PVR, Soetaert K, Solan M, Thrush S and others (2018) Global carbon cycling on a heterogeneous seafloor. Trends Ecol Evol 33:96–105

Solan M, Bradley J, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004a) Extinction and ecosystem function in the marine benthos. Science 306: 1177–1180

Solan M, Wigham BD, Hudson IR, Kennedy R and others (2004b) *In situ* quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. Mar Ecol Prog Ser 271:1–12

Southwood TRE (1988) Tactics, strategies and templets. Oikos 52:3–18

Spalding M, Fox HE, Allen GR, Davidson R and others (2007) Marine Ecoregions of the World: a bioregionalization of coastal and shelf areas. BioScience 57: 573–583

Steadman D, Thomas JB, Villanueva VR, Lewis F and others (2021) New perspectives on an old fishing practice: scale, context and impacts of bottom trawling. https://our-sharedseas.com/new-perspectives-on-an-old-fishing-practice/

Stearns S (1992) The evolution of life histories. Oxford University Press, New York, NY

Thioulouse J, Dray S, Dufour AB, Siberchicot A, Jombart T, Pavoine S (2018) Multivariate analysis of ecological data with ade4. Springer Verlag, New York, NY

Timmermann K, Banta GT, Glud RN (2006) Linking *Arenicola marina* irrigation behavior to oxygen transport and dynamics in sandy sediments. J Mar Res 64:915–938

Tseng LC, Huang SP, Das S, Chen IS, Shao KT, Hwang JS (2019) A slender symbiotic goby hiding in burrows of mud shrimp *Austinogebia edulis* in western Taiwan. PLOS ONE 14:e0219815

Tyler EHM, Somerfield PJ, Vanden Berghe E, Bremner J and others (2012) Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. Glob Ecol Biogeogr 21:922–934

van Wesenbeeck BK, van de Koppel J, Herman PMJ, Bakker JP, Bouma TJ (2007) Biomechanical warfare in ecology: negative interactions between species by habitat modification. Oikos 116:742–750

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301

Villéger S, Novack-Gottshall PM, Mouillot D (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. Ecol Lett 14:561–568

Villnäs A, Hewitt J, Snickars M, Westerbom M, Norkko A (2018) Template for using biological trait groupings when exploring large-scale variation in seafloor multifunctionality. Ecol Appl 28:78–94

Violle C, Jiang L (2009) Towards a trait-based quantification of species niche. Plant Ecol 2:87–93

Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74:159–164

Wilson JB (2012) Species presence/absence sometimes represents a plant community as well as species abundances do, or better. J Veg Sci 23:1013–1023

Woodin SA (1978) Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology 59: 274–284