Comparing taxonomic and functional trait diversity in marine macrozoobenthos along sediment texture gradients

Joao Bosco Gusmao [a,b], David W. Thieltges [c], Rob Dekker [c], Laura L. Govers [c,d], Kasper J. Meijer [d], Britas Klemens Eriksson [d,*]

[a] Programa de Pós-Graduação em Geoquímica: Petróleo e Meio Ambiente (POSPETRO), Institute of Geosciences, Federal University of Bahia (IGEO, UFBA), Salvador, BA, Brazil
[b] Environmental and Marine Biology, Åbo Akademi University, Åbo, Finland
[c] NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, Den Burg, Texel, Netherlands
[d] Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, Netherlands

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ABSTRACT

The rapid reorganization of global biodiversity has triggered an intense research effort to understand its consequences for ecosystem functioning. However, efforts to monitor biodiversity change and evaluate the outcomes for ecosystem states and processes are currently poorly aligned. While most monitoring programs evaluate ecosystem status by reporting measures of taxonomic diversity, it is not the number of species but rather the exhibited traits of these species that regulate function. Trait-based approaches assume that trait diversity and variability relate to changes in functions across environmental gradients, but this relationship remains to be explored for most marine benthic ecosystems. Using macrozoobenthic communities from the Dutch Wadden Sea as a model, we compiled information on traits related to animal-sediment relationships. This trait information was then combined with species' abundance data from a 19 years-long database to calculate different taxonomic and functional metrics that reflect macrozoobenthic diversity, function, and community structure. Finally, we compared how these taxonomic and functional metrics change along with sediment texture gradients. Our analyses showed that the structure of macrozoobenthic communities and various diversity metrics all changed with sediment gradients. The observed changes in the communities' species composition were associated with directional shifts in the relative presence of specific functional traits with increasing sediment grain size, from communities dominated by small body size, deposit-feeding, and short life span to communities characterized by large to medium body size, suspension-feeding, and long life span. We observed limited functional redundancy and high sensitivity of functional trait-based measures to changes in the community composition along sediment gradients. Our findings suggest that a trait-based approach provides valuable information about the ecological function of marine macrozoobenthic species complementary to traditional biodiversity measures (e.g., species richness, Simpson diversity, etc.). Hence, these measures may be used to characterize changes in ecosystem functioning in time and space using traditional monitoring datasets.

1. Introduction

The state of planetary biodiversity is under increasing pressure from global change (Newbold, 2018; Nunez et al., 2019; Worm and Lotze, 2021). Concerns about the erosion of species diversity and the consequences for ecosystem services and functions have triggered an intense research effort to understand the intrinsic value of biodiversity (Cardinale et al., 2012). Collective experimental evidence now shows that biodiversity has major implications for ecosystem functioning and that biological diversity is a key driver of biomass productivity in nature (Cardinale et al., 2006; Duffy et al., 2017; Tilman et al., 2014). Accordingly, policymakers have acknowledged the need to incorporate biodiversity in monitoring programs to document changes and evaluate ecosystem states using biological indicators (CBD Secretariat, 2010; Tittensor et al., 2014). However, monitoring biodiversity change and assessing changes in biological function is no trivial feat (Hillebrand

et al., 2018). Most monitoring programs only report measures of taxonomic diversity, but it is not the number of species per se that regulates function. Instead, the variety of attributes expressed by the different species modulates ecosystem states and processes (Hooper et al., 2005; Norberg, 2004). Currently, there is no consensus on how to monitor biodiversity such that functional properties of ecosystem states and changes are captured. Besides, there is an increasing realization that trends in the number of species do not adequately represent the current dynamics of biodiversity change (Eriksson and Hillebrand, 2019).

Trait-based approaches have been proposed as a way forward to better assess biodiversity effects on ecosystem states, on the assumption that trait diversity and variability are directly related to changes in functions across environmental gradients (Bremner et al., 2006; Duffy et al., 2015). Such an approach enables the comparison of putative ecological differences among species. This may thus capture their general functional role in an ecosystem and estimate the function of communities (Gagic et al., 2015; Norberg, 2004). Functional diversity is a measure based on trait distributions that gives a general overview of the variation in the functions performed by different species in an ecological system (Díaz and Cabido, 2001; Petchey and Gaston, 2006). It is expressed by the diversity of functional traits, which are any organismal characteristics related to an 'individual's' performance (i.e., survival, growth, and reproduction success) directly or indirectly related to one or more ecosystem functions or processes (Mlambo, 2014). Functional diversity is highly related to the maintenance of ecosystem functions, such as productivity (Díaz and Cabido, 2001; Hooper et al., 2005; Tilman, 2001) and resilience to disturbances or invasions (Dukes, 2001; Mouillot et al., 2013; Villéger et al., 2008). Therefore, indices based on functional traits are considered more informative or sensitive than taxonomy-based indices to capture ecosystem function (Díaz and Cabido, 2001; Gagic et al., 2015; Mokany et al., 2008). Trait-based ecology has thus grown strong in the past years, and the relationships between taxonomic and functional diversity and ecosystem functions have increasingly been explored in aquatic and terrestrial systems (Gerisch et al., 2012; Morais et al., 2019; Schirmel and Buchholz, 2013).

In marine soft-bottom environments, essential functional aspects of biodiversity are related to animal-sediment relationships. Despite their monotonous appearance, marine soft-bottom environments can vary in their physical and biogeochemical structure, providing microhabitats that result in diverse communities (Gray and Elliott, 2009). Aspects of sediment texture, such as grain size and mud content, are well known to drive the occurrence and abundance of species living in or on marine sediments, and species usually show ecological optima related to specific sediment texture (Compton et al., 2013a, 2013b; Johnson, 1971). While sediment texture is undoubtedly a strong driver of species occurrence and abundance in marine soft-bottom environments, infaunal organisms can, in turn, also affect the sediment and play an important role in promoting heterogeneity, thereby altering the ecological functioning of soft-bottom environments (Bremner et al., 2006; Eriksson et al., 2010; Reise, 2002; Snelgrove, 1998). For example, species that promote bioturbation influence sediment stability and alter the physical and biogeochemical characteristics of the substrate. Such changes impact other sediment-dwelling organisms and have implications for sediment metabolism and water–sediment chemical exchange (Govers et al., 2014; Kristensen et al., 2012; Lohrer et al., 2004). While the relationship between sediment texture and the distribution of individual species in marine sedimentary environments is well-known for bivalves (Compton et al., 2008) and annelids (Wouters et al., 2018), much less is known about the relationship between sediment texture and the taxonomic and functional diversity of entire communities in these environments. In addition, it is still discussed whether taxonomic and functional diversity measures are interchangeable or complementary in describing animal-sediment relationships. Therefore, our understanding of how benthic communities are structured would be favored by analytical approaches that combine information about the functional role of species in soft-bottom environments with taxonomic diversity measures at the community level.

Sedimentary marine environments with diverse invertebrate communities such as the Wadden Sea represent an ideal model to address research questions about animal-sediment relationships. The Wadden Sea is a long and shallow estuarine system protected by a chain of barrier islands that extends along >500 km, from the Netherlands to Denmark (de Jonge et al., 1993). It is connected to the North Sea via numerous inlets and its geomorphological features, mostly dominated by wetlands, tidal channels, and sand and mud flats, are largely controlled by wind and tidal regimes (de Jonge et al., 1993). This heterogeneous and highly dynamic sedimentary seascape provides a wide range of habitats for macrozoobenthic organisms (Beukema, 1976; Compton et al., 2013a, 2013b). Since the ecology of the Wadden Sea has been largely studied, there is abundant literature about the biology of its macrozoobenthic species, which allows the creation of complete databases about species' biological traits and the development of studies using a trait-based approach.

This study investigated animal-sediment relationships in marine macrozoobenthic communities by assessing taxonomic diversity and functional trait diversity along sediment texture gradients. We first constructed a functional trait matrix for invertebrates living in shallow marine sediments based on traits associated with animal-sediment relationships. This matrix was then used to construct a functional trait space (i.e., a multivariate representation of how different trait categories vary among species) of the macrozoobenthic communities. Using this trait space and a data subset from a long-term macrozoobenthic sampling program in the western Dutch Wadden Sea (Beukema & Dekker, 2020), we then assessed how taxonomic diversity, trait-based functional metrics, and community composition (expressed by changes in species and traits across stations) vary along with sediment texture gradients.

2. Methods

2.1. Sampling

All samples were taken on the tidal flats of Balgzand (52°55′N 4°49′E), an approximately 50 km^2 intertidal area located next to the Marsdiep inlet in the westernmost part of the Wadden Sea, a sheltered coastal system characterized by a landscape of barrier islands and tidal flats that extends from the Netherlands to Denmark (Lotze et al., 2005; Reise, 2005). The sampling was conducted in a long-term sampling program of the NIOZ Royal Netherlands Institute for Sea Research starting in the 1970 s (Beukema and Dekker, 2020). Samples were collected annually during winter at 15 fixed stations (twelve 1000 m-long transects and three quadrats of 900 m^2) distributed within Balgzand. On each 1000 m-long transect, 50 cores of 0.019 m^2 were taken (to a depth of about 30 cm) separated by 20 m. The five cores of each 100-m stretch were lumped, providing ten samples per transect. In addition, at each of the three quadrats of 900 m^2, nine samples of 0.105 m^2 were taken (to a depth of 30 cm). The total sampled area was 0.95 m^2 for both transects and plots. The samples were sieved out in the field through a 1 mm mesh sieve, and species were sorted alive and identified in the laboratory. Then, species biomass was quantified using ash-free dry weight (AFDW) per m^2 for each transect. For more details on the monitoring program, see Beukema and Dekker (2020).

Extra sediment samples were taken to quantify sediment grain size and silt content at all transects and quadrats. For transects, these samples were ~ 5 cm deep and taken at each of the 100 m stretches. Two subsequent sediment samples were pooled, thus providing five separate sediment samples per transect. For the permanent quadrats, two sediment samples were taken. The sediment grain size was quantified using a particle size analyzer (Coulter-counter) and expressed as the median grain size. Silt content was estimated using the pipette method (Gee and Bauder, 1986) and given as percentages of the total weight of sediment samples. Sediment texture (silt content and median grain size) was quantified from 2000 onwards, and we used only data from years with

available sediment information (years 2011, 2013, 2014, and 2016 were not considered due to lack of sediment data).

2.2. Macrozoobenthic function and diversity

Species richness and Simpson's diversity index were used as taxonomy-based metrics of macrozoobenthic diversity. Macrozoobenthic function-based metrics were assessed by calculating functional diversity indices and a specific metric for bioturbation potential. All taxonomic and functional metrics were calculated using species' biomasses (AFDW). For all analyses, we used the 15 fixed stations as our basic spatial replicate units, i.e., we lumped sub-samples of each station by calculating the total biomass per species per station. Since there was minimal variation in sediment texture among sub-samples within each station, we considered each station to represent a specific sediment texture type along the full gradient in our study area. Likewise, there was a relatively slight variation in sediment texture among years at each station and no overall temporal trend in sediment texture (Fig. S1). Thus, we considered the multiple samples from different years per station to be independent temporal replicates of specific sediment texture types.

For the functional diversity analysis, a functional trait matrix was generated (See Appendix 1) by classifying the species according to six functional traits (Table 1) that are associated with animal-sediment relationships in macrozoobenthos: bioturbation type, depth penetration in the sediment (in cm), adult body size (in mm), longevity (in years), feeding mode, and relative adult mobility (adapted from Jones & Frid 2009). Thus, a functional diversity index applied to such a set of traits would reflect the diversity of ways macrozoobenthic species can modify and interact with their sedimentary habitat. The six traits were further subdivided into modalities representing the range of variation for each functional trait (Appendix 1). We used fuzzy coding (Chevenet et al., 1994), ranging from 0 to 3, to classify each species according to its association with each functional trait modality. The information about species traits was collected from online databases (Faulwetter et al., 2014; MarLIN, 2006) and literature (e.g., Donadi et al., 2015a, 2015b; Jumars et al., 2015; Queirós et al., 2013; van der Zee et al., 2015). When information was not available for a particular species, trait scores were assigned considering the information about a closely-related species or the general information available for Genus or Family.

The functional trait space of the macrozoobenthic communities was represented by using a principal components analysis (PCA) on the fuzzy-coded trait matrix. The PCA was performed using on untransformed trait scores, excluding species with less than one occurrence, using tools of the R package *vegan* (Oksanen et al., 2020).

We estimated functional diversity by calculating Rao's Quadratic Entropy (Rao's Q), a widely used measure of functional trait diversity (Botta-Dukát, 2005; Botta-Dukát and Czúcz, 2015; Schmera et al., 2016). This index is based on the communities' functional trait space, a multivariate space represented by the pairwise Euclidean distances of species functional traits. Rao's Q measures the trait-based differences among species within a community, weighed by species biomass (or abundances). Rao's Q was calculated using the *dbFD* function in the R package *FD* (Laliberté and Shipley, 2011).

Finally, we calculated the bioturbation potential (BPc) of the community according to Solan et al. (2004) and Queirós et al. (2013). Bioturbation potential takes into account three main biological traits known to influence bioturbation activity: body size (expressed by the ratio biomass:abundance), mobility (*Mi*), and type of sediment reworking (*Ri*). *Mi* and *Ri* values (from 0 to 3 and 0 to 4, respectively) reflect the species' capacity to affect sediment structure. Bioturbation potential (BPc) was calculated with the formula:

$$BPc = \sum_{i=1}^{n} \left(\sqrt{Bi/Ai} \times Ai \times Mi \times Ri \right)$$

Bi and *Ai* are the biomass and abundance of species/taxon *i* in a

Table 1

Description of each category of each functional trait considered in the trait-based analyses. The complete table with the trait scores assigned for each species is available in the appendix 1.

Trait	no.	Modality
Bioturbation mode	1	Epifauna
	2	Biodiffuser: fauna that randomly moves sediment over short distances causing diffusive mixing (François et al. 1997).
	3	Surficial modifiers: Any invertebrate whose sediment reworking activity is restricted to the uppermost (~1 cm) sediment layers (Solan et al. 2004).
	4	Upward-conveyor: head-down oriented fauna which causes active sediment movement from depth to the surface (François et al. 1997).
	5	Downward-conveyor: head-up oriented fauna which causes active sediment movement from the surface to depth through their gut (François et al. 1997).
	6	Regenerator: an invertebrate that transfers sediment at depth to the surface where it is washed away and replaced by the sediment of surficial signature (Gardner et al., 1987)
Depth in the sediment/ burrowing capacity	1	Surface
	2	0 and ≤ 3 cm
	3	>3 and ≤ 8 cm
	4	>8 and ≤ 15 cm
	5	>15 and ≤ 25 cm
	6	> 25 cm
Body size (adults)	1	≤ 5 mm
	2	>5 and ≤ 10 mm
	3	>10 and ≤ 20 mm
	4	>20 and ≤ 40 mm
	5	>40 and ≤ 80 mm
	6	>80 and ≤ 160 mm
	7	> 160 mm
Feeding mode	1	Deposit-feeder
	2	Suspension-feeder
	3	Opportunist/scavenger
	4	Grazer (including selective feeding on benthic microalgae)
	5	Predator/carnivore
Longevity	1	≤ 1 year
	2	>1 and ≤ 3 years
	3	>3 and ≤ 6 years
	4	>6 and ≤ 10 years
	5	> 10 years
Adult movement	1	Sessile
	2	Swimmer
	3	Crawler
	4	Burrower/Tube dweller

sample, respectively. Trait scores of *Mi* and *Ri* were obtained from Queirós et al. (2013).

2.3. Data analysis

Both sediment grain size and silt content were used as predictors in our uni- and multivariate analyses because sediment grain size was highly variable in sediments with low silt percentage (Figure S2). All analyses and graphs were generated in the R 4.1.1 programming environment (R Core Team, 2021).

We used generalized additive model (GAM) fits to visualize the general trends of macrozoobenthic biomass, diversity, and functional metrics along sediment texture gradients (i.e., median grain size and silt content). The fitted GAMs were based on a Gaussian distribution with the number of basis functions of smooth terms restricted to four (k = 4) to limit the curve's wiggliness. GAMs were fit using tools in the R package *mgcv* (Wood, 2019). The correlations among diversity and functional metrics were assessed using generalized pair plots (Schloerke et al., 2021).

Changes in community multivariate structure, expressed by the

variation in species abundances and composition across sample units, were analyzed using a distance-based approach. A species' biomass per sample matrix (from now on referred to as "biomass matrix") was square-root transformed and used to calculate a Bray-Curtis resemblance matrix to represent changes in the community's species structure. To analyze the communitýs trait structure, we multiplied the biomass matrix by the fuzzy-coded trait matrix (Bremner et al., 2006). This matrix multiplication resulted in a biomass-weighted trait-by-sample matrix, which was then used to calculate a Bray-Curtis resemblance matrix. Since we had a priori assumptions regarding the effects of sediment texture and macrozoobenthic community structure, we used canonical analysis of principal coordinates (CAP) to analyze how community structure (both species and trait-based, expressed by Bray-Curtis resemblance matrices) change along with sediment grain size and silt content. CAP is a distance-based ordination technique that uses a model framework to find the canonical axes that best explain the variation in the multivariate structure along with one or more assumed predictors (Anderson and Willis, 2003). We performed a separate CAP analysis for species and functional traits for each environmental predictor. The CAPs were performed using the *capscale* function in the R package *vegan* (Oksanen et al., 2020). Finally, we complemented the CAP results with permutation tests performed on 999 permutations using the *anova.cca* function in the R package *vegan* (Oksanen et al., 2020). Additionally, we checked for differences in the multivariate dispersion within stations between species and trait-based ordinations. We used the *betadisper* function in the package *vegan* (Oksanen et al., 2020) to calculate the average distance to the stations' centroids within a multivariate space (i. e., principal coordinates of Bray-Curtis distances). These average distances to centroids were then compared between species and trait-based analysis using a *t*-test.

Changes in trait dominance along with sediment texture gradients were assessed using stacked area plots. These plots were based on predicted values of GAM smooth lines of biomass-weighted trait scores. Stacked area plots were made using the R packages *mgcv* (Wood, 2019) and *ggplot2* (Wickham, 2009).

3. Results

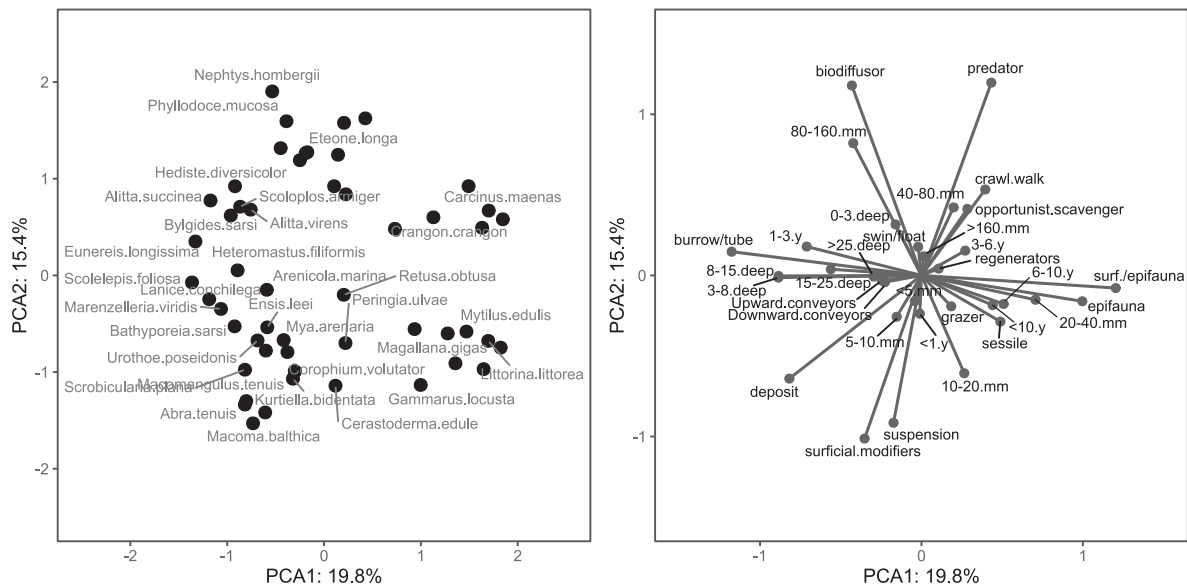### 3.1. Functional trait space of macrozoobenthos communities

The PCA ordination of the multivariate functional trait space constructed from 55 species whose biomasses were quantified is depicted in Fig. 1. The first two axes explained >35 % of the total variation of the trait space (Table 2), which was defined mainly by bioturbation type, body size, and diet (Fig. 1). The first axis separated species with traits related to deep burrowing and tube building (negative scores; e.g., *Scolelepis foliosa, Arenicola marina, Eunereis longissima*) from epifaunal species (positive scores; e.g., *Mytilus edulis, Magallana gigas, Littorina littorea*). The second axis separated large-body, biodiffusors, and predatory behavior (positive scores; e.g., *Nephytys hombergii*) from suspension and deposit feeding, and surficial modifiers (negative scores; e.g., *Macoma balthica, Cerastoderma edule, Corophium volutator*).

### 3.2. Changes in diversity metrics along sediment texture gradients

All metrics used to describe macrozoobenthic biomass, diversity, and function showed notable changes along gradients in sediment properties (Fig. 2, Table S1). However, there was a distinct difference in the relationship between species richness and biomass on the one hand and biomass-based diversity and functional trait indices on the other (Table S1). Species richness and total biomass presented a unimodal quadratic relationship with the grain size gradient (Fig. 2a,e) and a decreasing trend with increasing silt percentage in the sediment (Fig. 2b, f). Simpson diversity and Rao's Q were negatively related to increasing grain size (Fig. 2d,i) and positively associated with increasing silt

Table 2
Summary of the results of the first four principal components of the PCA representing the functional trait space of macrozoobenthic community.

	PC1	PC2	PC3	PC4
Eigenvalue	8.75	6.80	5.89	4.14
Proportion Explained	0.20	0.15	0.13	0.09
Cumulative Proportion	0.20	0.35	0.49	0.58
Total inertia: 44.1				

Fig. 1. Functional trait space of macrozoobenthic communities from the Dutch Wadden Sea, constructed from a PCA based on fuzzy scores of assigned trait categories. Left panel: species distribution in the functional trait spaces with the names of the most common species (abundance > 50 individuals). Right panel: vectors of each functional trait category in the trait space used for the analysis. Trait label suffixes:.deep = depth in sediment,.y = years,.mm = body size in mm. Complete trait names, categories, and descriptions are shown in Table 1.
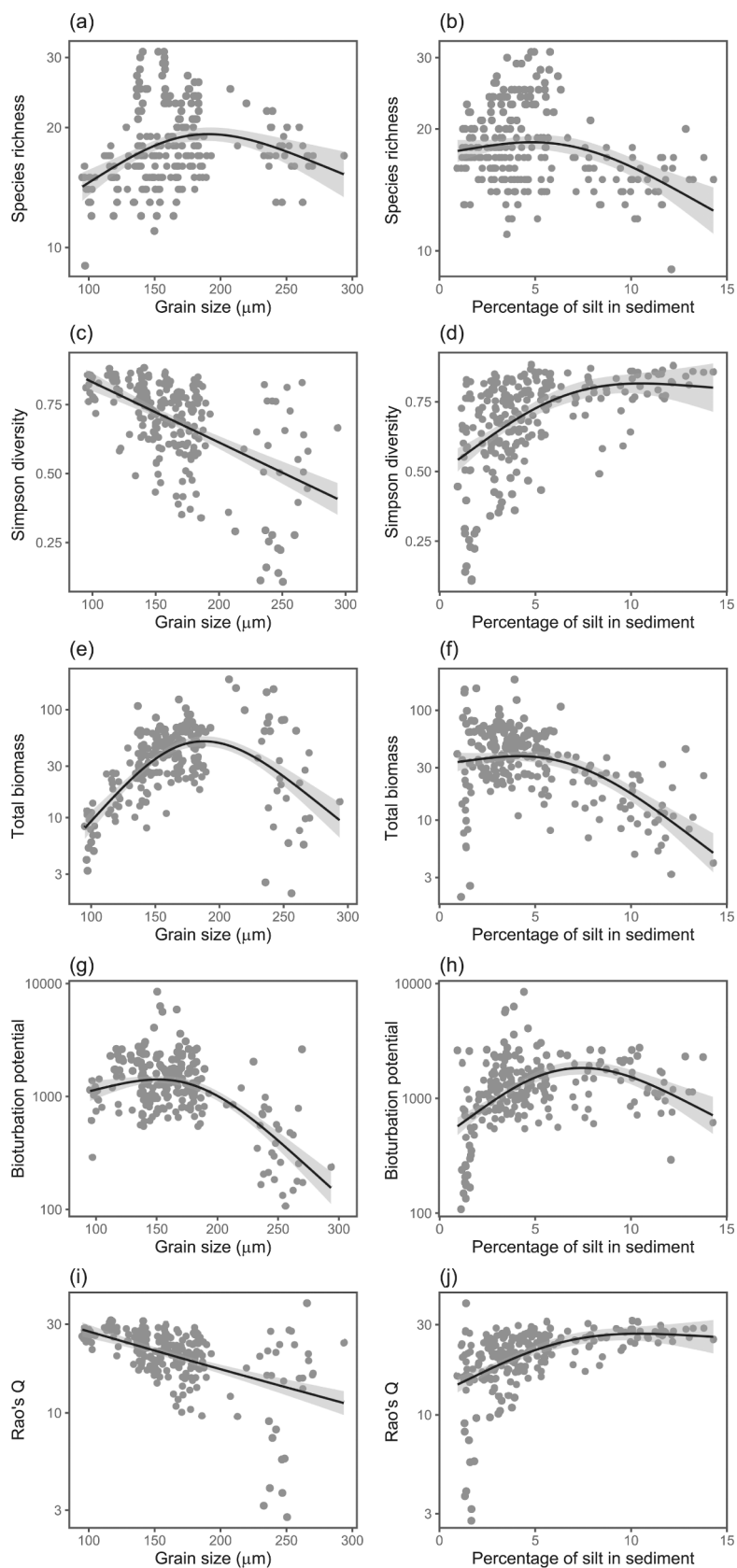
Fig. 2. General trends of macrozoobenthic diversity and function along gradients in sediment texture. Black lines are GAM smooths based on four basis functions. Gray shades are the 95% IC of GAM smooths.

percentage (Fig. 2e,j). Community bioturbation potential showed a decreasing trend with sediment texture (Fig. 2g), but depicted a unimodal quadratic relationship with silt percentage (Fig. 2h). The variation trends observed for Rao's Q and Simpson diversity reflected their high correlation, the highest among the analyzed metrics (Pearson correlation = 0.897, Fig. 3). These indices also showed a relatively high negative correlation with total biomass (Pearson correlation = >0.45, Fig. 3). Species richness was positively correlated with total biomass (Pearson correlation = 0.353, Fig. 3), which explains their similar responses to sediment texture (Fig. 2).

3.3. Species- and trait-based community structure changes along sediment texture gradients

The macrozoobenthic community structure changed along the sediment texture gradient for species- and trait-based analyses (Fig. 4). Although sediment texture explained less than 20 % of the total variation in community structure, its effect was significant in all tested cases (Table 3). The transects differed clearly in their sediment characteristics, especially for grain size. This separation was consistent through time, as demonstrated by the clustering of the site scores for individual stations along the x-axis (Fig. 4). Notably, the variation in assembly structure for

each station was much higher for the trait-based than the species-based ordination (Fig. 4). Indeed, the multivariate dispersion of stations was significantly higher for trait-based multivariate space compared to the species-based space (t = 3.8097, df = 27.3, p-value less than 0.001).

3.4. Trait changes underlying shifts in functional diversity along sediment texture gradients

The observed changes in trait structure along sediment texture gradients were explained mainly by changes in the dominance of specific trait modalities related to bioturbation behavior, body size, diet, and longevity (Fig. 5 and S3). Coarser sediments were dominated by suspension-feeding, surface modifiers, large-body sizes, and long life spans (Fig. 5 and S3). Finer sediments with high organic matter content were dominated by deposit-feeding, small body sizes, short life spans, and a wider range of bioturbation modalities (Fig. 5 and S3).

4. Discussion

Trait-based diversity measures are a promising approach to understanding the functional consequences of biodiversity change but how these measures relate to changes in function across environmental
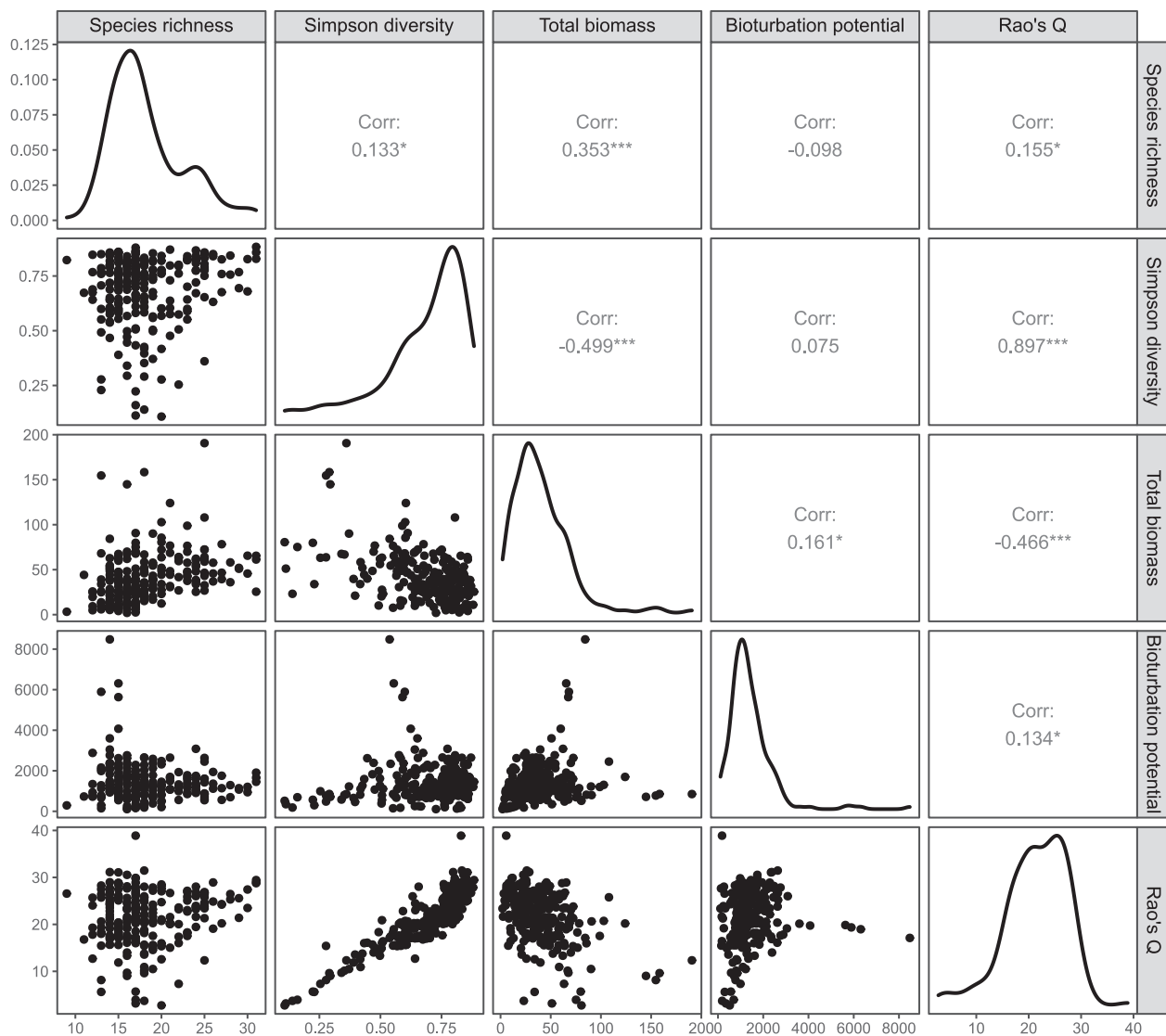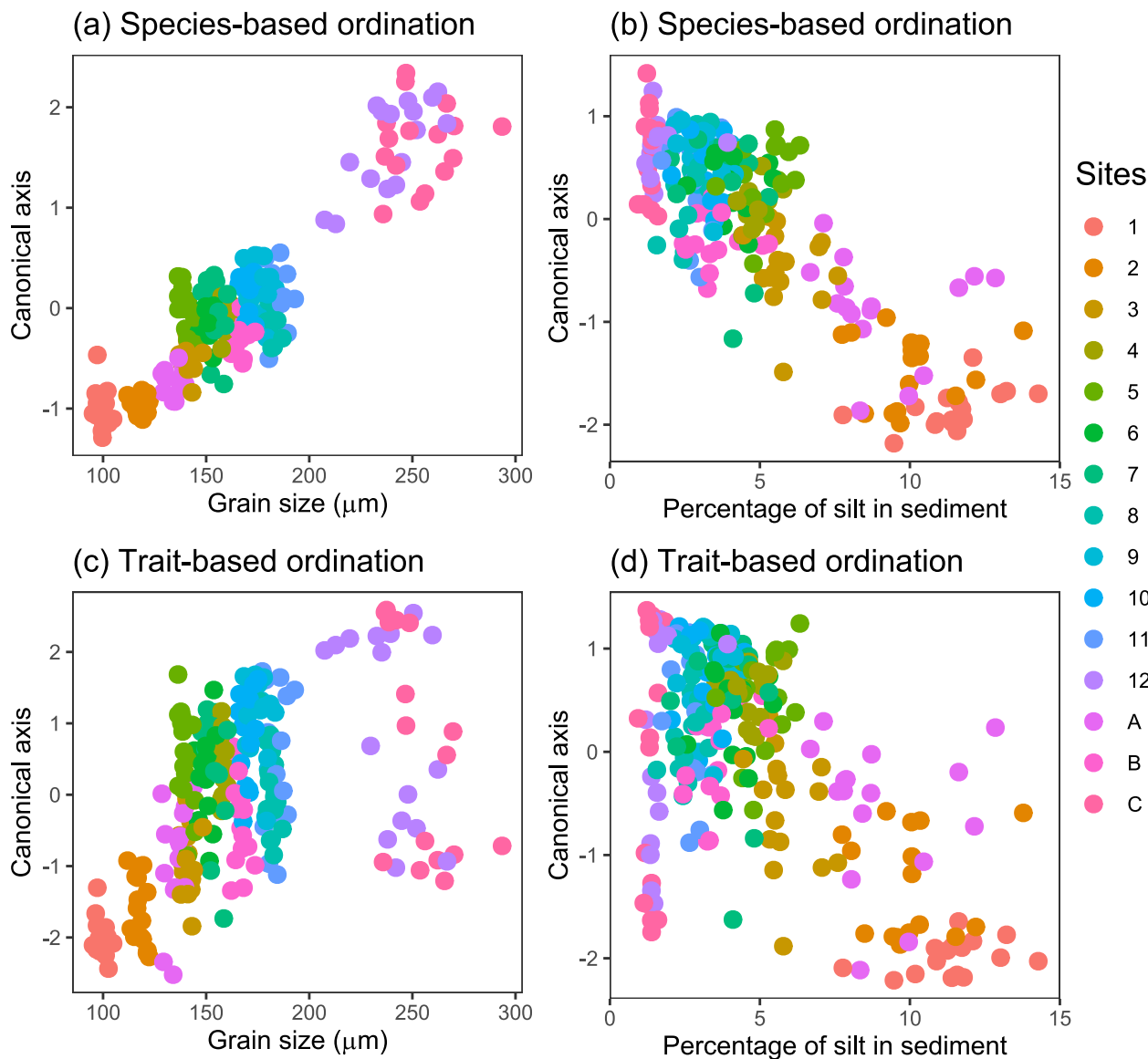

Fig. 3. Generalized pair plot depicting scatterplots and Pearson's correlations of the paired combinations of diversity and functional metrics describing macrozoobenthic communities. Diagonal graphs indicate the density distributions of each metric's values.

Fig. 4. Canonical axes of CAP ordinations depicting changes in species (a-b) and trait (c-d) structure of macrozoobenthic communities along sediment texture gradients.

Table 3
Summary of the permutation tests performed on the CAP results testing the effect of sediment texture predictors on the structure of macrozoobenthic communities. Analyses were performed on 999 permutations. CAP ordinations are shown in Fig. 2.

Ordinations		df	SS	pseudo-F	p-value
Species-based					
CAP:	Grain size	1	7.96	28.81	**0.001**
	Residual	238	65.80		
CAP:	Silt %	1	8.05	29.16	**0.001**
	Residual	238	65.71		
Trait-based					
CAP:	Grain size	1	2.15	16.35	**0.001**
	Residual	238	31.32		
CAP:	Silt %	1	4.93	41.09	**0.001**
	Residual	238	28.55		

along sediment texture gradients. Trait-based analyses indicated higher variability in community structure than species-based analyses. There was a directional change in community function with increasing sediment grain size from small short-lived sediment-reworking infauna to large long-lived suspension-feeding infauna. All diversity metrics were significantly related to sediment properties but differed in pattern: species richness and bioturbation potential depicted a unimodal trend with increasing sediment grain size, while Simpson's diversity and Rao's Q index showed a monotonic decrease. Our results suggest strong links between taxonomic and functional trait diversity of communities along sediment texture gradients and indicate that the different diversity metrics capture complementary aspects of this relationship.

4.1. Diversity and functional metrics

Species- and trait-based metrics captured different facets of community diversity. However, all metrics changed with sediment gradients, suggesting strong links between community diversity and sediment properties that probably result from the following mechanisms. The unimodal trend of species richness along sediment texture gradients,

gradients remains to be explored for most marine ecosystems. Our results showed that the structure of macrozoobenthic communities, expressed by both its taxonomic and functional trait structure, changed

with a peak at intermediate grain sizes, probably stems from the distribution of species associated with finer or coarser sediments that overlap in distribution to a certain extent at intermediate sediment grain sizes (Anderson, 2008). However, when corrected for biomass in the form of Simpson's diversity index, species-based diversity declined with sediment grain size and increased with silt content. Given the limited redundancy in function of the species in the communities, it is inevitable that Rao's Q, which also considers the relative biomasses of species in a community, also showed a similar monotonic pattern with sediment gradients. In contrast, the other functional trait-based index that we investigated, the bioturbation potential, showed a unimodal pattern similar to species richness. This may partly result from the fact that for the calculation of the bioturbation potential index, the values of each species in a community are simply summed up (see methods), which makes the index sensitive to the total number of species in a community (Queirós et al., 2013; Solan et al., 2004). With lower total species numbers in communities at both ends of the sediment gradients, our results are in line with classical conceptual models describing the relationships between macrozoobenthic diversity and the associated sediment activities (Rosenberg, 2001). Considering that we observed gradients in bioturbation-related traits along with sediment gradients, the similar trends of diversity and bioturbation potential are likely a reflection of the increased incidence (and biomass) of species with high bioturbation capacity (Kristensen et al., 2014; Solan et al., 2004).

4.2. Species-based community structure

The observed changes in species-based macrozoobenthic community structure along sediment gradients (Fig. 2) align with previous observations and are likely a universal phenomenon. For example, species-based community structures of benthic intertidal organisms in estuarine soft-sediments in northern New Zealand change with sediment's mud content (Anderson, 2008). These changes in species-based community structure along sediment gradients result from the fact that individual species are usually associated with different sediment characteristics (Anderson, 2008; Robertson et al., 2015; Ysebaert and Herman, 2002). As a result of these species-specific sediment associations, the total species community composition inevitably changes along sediment gradients. The underlying processes of species-specific sediment associations are complex and include, among others, settlement preferences (Butman, 1987), species interactions such as competition and predation (Brenchley, 1982; Peterson and Skilleter, 1994; Wilson, 1991), and physical disturbances (Thrush and Dayton, 2002). In addition, species themselves can also affect sediment characteristics, for example, by bioturbation, which influences sediment stability and alters the physical and biogeochemical properties of the sediment (Eriksson et al., 2010; Meysman et al., 2006; Reise, 2002; Snelgrove and Butman, 1994). Hence, disentangling the causes and effects of animal-sediment relationships is not easy (Snelgrove and Butman, 1994) and practically impossible with the correlative data used in our analyses.

4.3. Trait-based community structure

Like the species-based community structures, functional trait-based community structures also changed along sediment gradients in our analyses (Fig. 2). Thus, the changing species composition along sediment gradients was accompanied by changes in species functional traits, which affected the function of the community as a whole. Indeed, the relative presence of the different trait categories within communities showed distinct directional changes along the sediment texture gradients, especially for bioturbation behavior, body size, diet, and longevity (Fig. 3 and Fig. S3). This directional change in specific traits resulted in a general shift in community function with increasing sediment grain size, from small short-lived sediment-reworking deposit-feeding infauna to large long-lived suspension-feeding infauna. Such links between specific traits and sediment texture are well known, in particular regarding

feeding modes, where shifts from suspension to deposit feeders in finer sediments are well documented and considered to be related to the increased availability of organic matter in finer sediments (Gray and Elliott, 2009; Pearson and Rosenberg, 1978; Seitz and Lipcius, 2001). Hence, our analyses suggest that the directional changes of trait-based community structures that we observed along sediment gradients captured functional changes in the communities.

4.4. Comparing species- and trait-based approaches

Although species- and trait-based changes in community structure showed similar responses to gradients in sediment texture in our analyses, the trait-based approaches showed a higher variability within sites than the species-based approaches (Fig. 2). This indicates that the functional trait-based approach captured functional differences in the community structure that were not picked up by the species-based approach. The mechanism underlying the higher sensitivity of the trait-based approach is probably a limited functional redundancy in the species present in the studied macrozoobenthic communities. If species are not equivalent in their ecological function and can vary significantly in their trait combinations (as indicated by the relatively wide distribution and limited overlap of species in the trait space, Fig. 1), small changes in species composition can lead to significant changes in the relative trait composition of a community (Darr et al., 2014; Micheli and Halpern, 2005). That the functional redundancy of the species in our study may indeed be relatively low is also suggested by the significant positive linear correlation between the functional diversity metric Rao's Q and the taxonomic richness metrics species richness and Simpson's diversity index (Fig. 5). A linear increase of functional diversity with species richness is the expected pattern if functional redundancy is low, while an asymptotic relationship would be expected if species' functional traits were redundant to a certain extent (Micheli and Halpern, 2005). In particular, for the Simpson's diversity index, which considers the relative biomasses of species in a community like Rao's Q, the correlation was strong and linear, suggesting a low functional redundancy (Micheli and Halpern, 2005; Schleuter et al., 2010). Hence, higher species diversity in a community will inevitably lead to higher functional diversity. However, this does not mean that taxonomic and functional diversity are equivalent as functional-trait based community structure and diversity metrics will strongly depend on the specific traits present in a community and not on the diversity of species per se (Mason et al., 2013; Schleuter et al., 2010; van der Plas, 2019). The species- and trait-based changes in community structure that we observed along sediments gradients thus capture different facets of the community diversity, even if the general direction of the changes looks similar at first sight.

5. Conclusions

Earth's ecosystems currently exhibit high rates of biodiversity change, highlighting the urgency of understanding the relationship between changes in communities and the function of our natural ecosystems (Blowes et al., 2019; Dornelas et al., 2014; Eriksson and Hillebrand, 2019; Hillebrand et al., 2018). Our results support that trait-based approaches are a way forward to assess the effects of biodiversity reorganization on ecosystem functioning. The limited functional redundancy and high sensitivity of functional trait-based measures to changes in the community composition across sediment gradients demonstrate that functional trait-based diversity measures provide valuable complementary information about the ecological function of marine macrozoobenthic communities. Thus, the functional trait approach complemented the traditional measures of diversity in addressing change, but they align better to answer questions of consequences for ecosystem functionality since they are directly related to changes in functions across environmental gradients (Bremner et al., 2006; Gagic et al., 2015; Norberg, 2004; Petchey and Gaston, 2006). This indicates
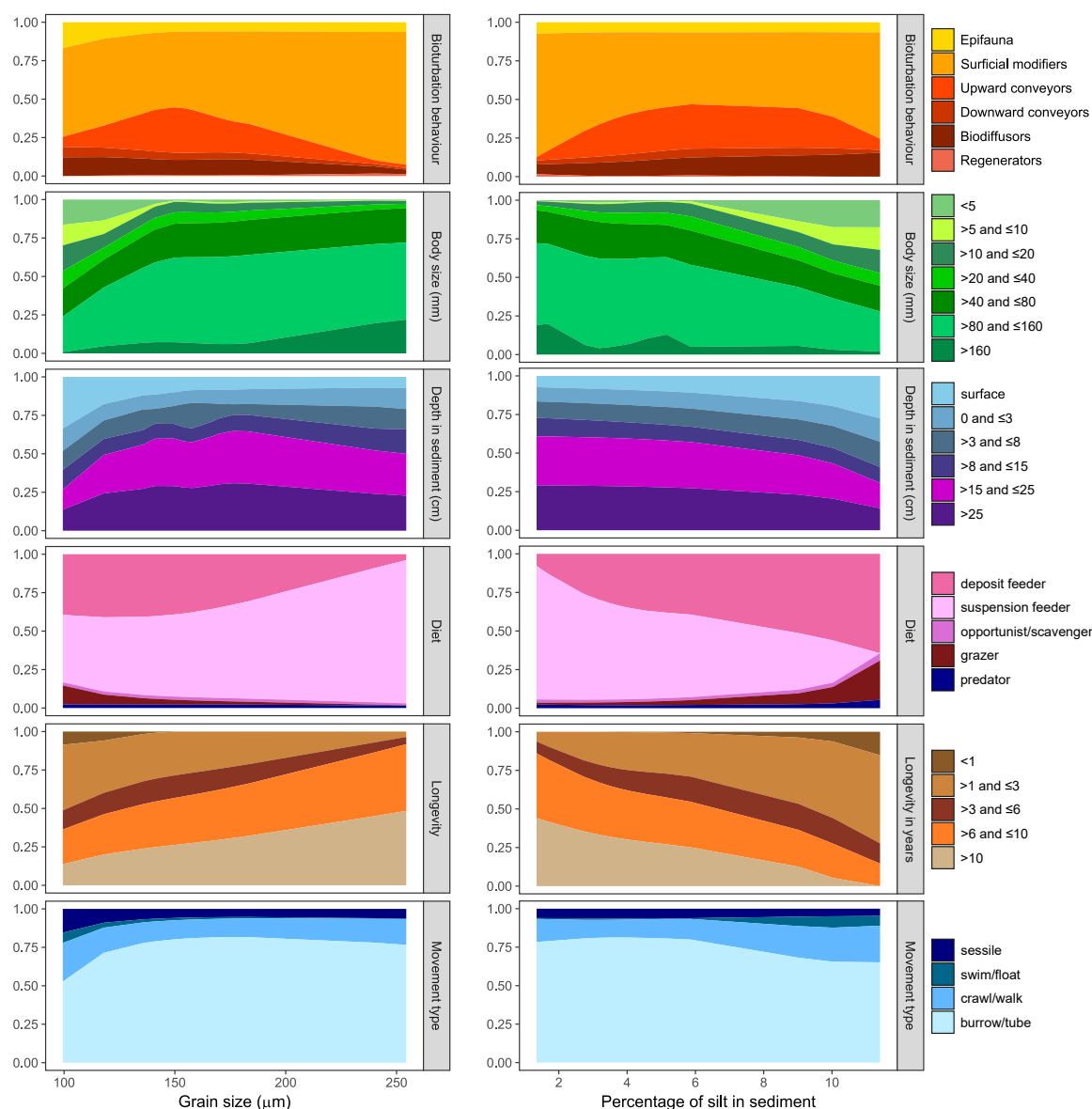
Fig. 5. Changes in the dominance of trait categories expressed by the relative biomass-weighted trait scores along sediment texture gradients (Left panels: median grain size; Right panels: percentage of silt content).

the potential of using trait-based methods to characterize changes in ecosystem function in space and time using traditional monitoring data. Marine systems exhibit the highest rates of species reorganization measured across biomes and realms (Blowes et al., 2019), and sedimentary systems dominate the Earth's surface. We, therefore, pledge an investment in understanding the functional aspects of marine organisms in sediment systems and for an increased effort in making marine monitoring data available to the scientific community.

CRediT authorship contribution statement

Joao Bosco Gusmao: Conceptualization, Formal analysis, Visualization, Writing – original draft. **David W. Thieltges:** Writing – original draft, Writing – review & editing, Supervision. **Rob Dekker:** Investigation, Data curation, Writing – review & editing. **Laura L. Govers:** Writing – review & editing. **Kasper J. Meijer:** Writing – review & editing. **Britas Klemens Eriksson:** Writing – original draft, Writing – review & editing, Supervision.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109718.

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