

Interregional comparison of benthic ecosystem functioning: Community bioturbation potential in four regions along the NE Atlantic shelf

Gogina Mayya ^{1,*}, Zettler Michael L. ¹, Vanaverbeke Jan ², Dannheim Jennifer ^{3,4}, Van Hoey Gert ⁵, Desroy Nicolas ⁶, Wrede Alexa ^{3,4}, Reiss Henning ⁷, Degraer Steven ², Van Lancker Vera ², Foveau Aurelie ⁶, Braeckman Ulrike ⁸, Fiorentino Dario ^{3,4}, Holstein Jan ⁹, Birchenough Silvana N.R. ¹⁰

¹ Leibniz Institute for Baltic Sea Research, Seestraße 15, 18119 Rostock, Germany

² Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Vautierstraat 29, B-1000 Brussels, Belgium

³ Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, P.O. Box 120161, D-27570 Bremerhaven, Germany

⁴ Helmholtz Institute for Functional Marine Biodiversity at the University of Oldenburg (HIFMB), Ammerländer Heerstraße 231, Oldenburg 26129, Germany

⁵ Flanders Research Institute of Agriculture, Fishery and Food, Ankerstraat 1, 8400 Oostende, Belgium

⁶ Ifremer, Laboratoire Environnement et Ressources Bretagne nord, 38 Rue du Port Blanc, 35800 Dinard, France

⁷ Faculty of Biosciences and Aquaculture, Nord University, 8049 Bodø, Norway

⁸ Marine Biology Research Group, Ghent University, Krijgslaan 281/S8, 9000 Gent, Belgium

⁹ Focke & Co., Siemensstraße 19, 27283 Verden, Germany

¹⁰ CEFAS Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, United Kingdom

* Corresponding author : Mayya Gogina, email address : mayya.gogina@io-warnemuende.de

Abstract :

Bioturbation is one of the key mediators of biogeochemical processes in benthic habitats that can have a high contribution to seafloor functioning and benthic pelagic coupling in coastal waters. Previous studies on bioturbation were limited to point locations and extrapolations in single regions, but have not accounted for regional differences under changing environmental conditions, though there are indications that species contributions will differ across regions or with biotic and abiotic context. To capture those differences and assess global patterns and commonalities, multi-regional analyses are imperative. Here for the first time, bioturbation potential (BPc), a functional indicator of benthic community bioturbation, was estimated based on macrofauna data from four regions (i.e. German Baltic Sea, German North Sea, Belgian part of the North Sea and the Eastern English Channel). For each region and sediment type we identified key species contributing to BPc. Comparison within and across regions demonstrated regional differences, and both overlap and mismatch between species that are functionally important and those that are dominant in biomass. Knowledge on the functionally important species is crucial when management objectives include the protection of certain ecosystem functions. Available environmental layers were used as predictors to model the spatial distribution of BPc for each area and to explore the underlying drivers of differences. Random forest models were trained using as response variables either i) BPc initially calculated per station; or ii) BPp – the species-specific contribution to BPc – for key species

(with subsequent summation of their predicted full-coverage distributions to BP_c). Maps of BP_c distribution predicted by random forest were compared with those generated using natural neighbour interpolation. Overall, derived BP_c values increased towards the German parts of the North and Baltic Seas. The relevance of BP_c for ecosystem processes and functions, however, vary with biotic and abiotic settings. Results revealed a strong association of BP_c with species diversity and region, but less with sediment grain size. A large range of BP_c occurred when species richness was low. This suggests that the provisioning of high bioturbation activity is possible also under low diversity, where it is vulnerable due to reduced resilience. The executed multi-regional analysis allowed identifying regional differences in performance of macrofauna, suggesting the need for region-specific conservation and management strategies.

Highlights

► First multi-regional analysis of macrofauna community bioturbation potential (BP_c). ► Functionally important key species differ regionally and between sediments. ► Overall BP_c values decreased from the Baltic Sea towards Eastern English Channel. ► Relevance of BP_c for ecosystem functions vary with biotic and abiotic settings. ► Results accent the need for region-specific conservation and management strategies.

Keywords : Macrofauna traits, Bioturbation index, Biogeographic comparison, Species distribution modelling, Biodiversity attributes, Ecosystem management

1. Introduction

Ecosystem properties are influenced by alterations in biodiversity (Snelgrove et al., 2018; Thomsen et al., 2019). Benthic systems regulate energy in marine ecosystems and grant valuable products and ecological services to human society (Paterson et al., 2012). Benthic macrofauna is important in food webs, sediment transport, benthic-pelagic coupling, nutrient cycling and other biogeochemical processes, both directly or indirectly, through regulating properties for microorganisms, enhanced physical exchange and physiological factors (Griffiths et al., 2017). Thus, presence or absence of specific traits due to species extinctions, invasions and changes in number of individuals or biomass loss will modify their contribution to ecosystem functioning. A number of previous studies suggested that species contributions will differ across regions and/or with under different environmental conditions (Godbold and Solan 2013; Wohlgemuth et al. 2017). Bioturbation is one of the main components of benthic-pelagic coupling in marine coastal ecosystems: it comprises all transport processes carried out by animals that directly or indirectly affect sediment matrices, including both particle reworking and burrow ventilation (Kristensen et al., 2012). Quantitative estimates of bioturbation are useful for comparison of varying effects of benthic organisms on ecosystem functioning, including those related to altered oxygen supply, chemical gradients within the sediment and solute fluxes at the sediment-water interface, microbial degradation rates, sediment and contaminant transport (Haider et al., 2019).

The bioturbation potential of a community (BP_c , Solan et al., 2004; ; Birchenough et al. 2012; Birchenough et al. 2013; Queirós et al., 2013) is one of the few existing quantitative trait-based indicators for ecosystem functioning. It combines particular traits of species (e.g., sediment reworking and mobility) with species abundance and biomass to infer species' function as bioturbator (Queirós et al., 2013). Hence, it can be calculated based on largely available benthic macrofauna data, in contrast to rarely and sporadically available data on bioturbation depth, bio-mixing models and biodiffusion coefficients measured in experimental set-ups (e.g. Soetaert et al., 1996; Morys et al., 2016, but see also the global bioturbation dataset recently published by Solan et al., 2019). These types of indicators, linked with pressures in a spatially explicit manner and at larger geographical scales, are often required for marine spatial planning and management purposes (Galanidi et al., 2016; Reiss et al., 2015). Although BP_c does not take into account context-specific bioturbation activities (Gogina et al., 2017; Aneiros et al., 2018), it has been successfully related to organic matter mineralisation processes (Braeckman et al., 2014) as well as fluxes of nutrient-species and oxygen across the sediment-water interface (Wrede et al., 2017). Even though many studies have extrapolated from point sources (Gogina et al., 2017; Meyer et al., 2019), they did not

account for interregional differences in activity or differences in behavior between locations or over time under changing conditions, stirring up our motivation to perform the first biogeographic comparison of BP_c patterns across regions.

The general goal of this study is to amplify our knowledge on BP_c by a comparative case study on large spatial scale comprising four regions along the European Shelf. This is especially necessary as this index is gaining more and more popularity, and even though BP_c was not invented for linking it with ecosystem functioning (Solan et al. 2004), it does link to it well in some environments, while in others it does not. The explanation is, that in the cases it does, BP_c reflects a process (e.g. particle displacement) that significantly contributes to the investigated ecosystem function, while in other areas it doesn't: e.g. fauna can be not (very) important (for mineralization processes) in coarse permeable sediments because of the advective currents going through the sediment, overruling biological transport effects (Braeckman et al. 2014). Nevertheless, the BP_c seems to have an additional value as ecological indicator in terms of assessing function, rather than only abundance or biomass.

Here we attempt to estimate how variations in sediment composition and inhabiting fauna could potentially affect the spatial distribution of BP_c , and hence the effect of macrofaunal communities on benthic biogeochemical processes. Comparing BP_c and key contributing species across biogeographical zones might reveal potential consequences of natural and anthropogenic pressures on these ecosystems.

To obtain full-coverage maps for each region, spatial modelling was based on observational biological data (disregarding temporal variation) linked to available sets of environmental parameters (Reiss et al., 2015). Thus, in order to assess spatial distribution of the processing, and how BP_c will vary with habitat type, this work aims to: (1) estimate BP_c and identify the key species contributing most to bioturbation in each region and in different sediment types; (2) assess the regional spatial differences and variability of ecosystem functioning expressed by modelled BP_c ; and (3) disentangle the drivers influencing those differences.

2. Materials and methods

2.1. Study regions

In order to account for regional differences, we focussed on four study sites located in the Baltic and the Atlantic biogeographical regions on the continental shelf, including the German part of the Baltic Sea (DEBS), the German part of the North Sea (DENS), the Belgian part of the North Sea (BENS) and the Eastern

English Channel (ENCH) (see the map in Supplementary material S1 for stations locations, and Table 1). Apart from regional proximity and availability of data, this choice of regions was expected to be particularly informative due to rather broad range of changing environmental conditions, including transition from north to south and from enclosed brackish Baltic Sea to more open offshore and exposed areas. Additionally, all four regions are sufficiently well studied (data availability) to allow meaningful interpretation of broad findings without disregarding the region-specific context. Moreover, the regions are located along the coastal areas that experience increasing pressure from both climate change and various human activities.

The German part of the Baltic Sea

The Baltic Sea is a semi-enclosed sea connected to the North Sea by two narrow shallow straits (the Belt Sea and the Sound). The restricted water exchange through the straits shapes environmental conditions in the entire Baltic Sea. It is highly stratified by strong vertical salinity and temperature gradients. Halocline depth is controlled by freshwater runoff, wind-induced mixing and advection and varies from 10 m to 30 m in shallower regions (Dargahi et al., 2017). In the south-western Baltic Sea (study area – 14800 km², average depth - 19 m) sedimentary habitats are mainly shaped by postglacial processes. Shallow areas along the shore and on top of the offshore glacial elevations are characterized by a mosaic of rocks, till, gravel and coarser sands. The substrate is finer with increasing water depth. Organic-rich muddy sediments dominate in the basins and deeper part of trenches (Darr et al., 2014). Near-bottom salinity and oxygen conditions are the main drivers of species richness and composition of benthic macrofauna communities in the area (Zettler et al., 2017). The overall salinity declines from 20-25 in the western part of Kiel Bay towards 7 in the eastern Pomeranian Bay. The water exchange between the western Baltic and the Baltic Proper is inhibited by the Darss and Drogden Sills, causing highest temporal variability of salinity in the western part of the study area. Aperiodic seasonal oxygen depletion events occur in the deeper areas of the Kiel Bay, the Bay of Mecklenburg and in the Arkona Basin, and have negative effects on the diversity and density of soft-bottom fauna (Arntz, 1981).

The German part of the North Sea

The study area in the south-eastern North Sea region is known as the German Bight. It covers an area of 28539 km² (German Exclusive Economic zone area, EEZ). The average depth is 30-40 m, covering shallow parts (e.g. the Amrum Bank) with 10 m depth and deeper areas (up to 60 m depth) in the Helgoland deep trench and the most northern tip of the German EEZ. In its shallower regions, the water column is generally well mixed, due to wave action and tidal currents, while deeper parts are stratified which results

in a high seasonal variability of bottom waters in different geographical regions. Most of the primary production occurs in the nutrient rich, well-mixed waters of the shallow southern parts and along the eastern coast. Salinity ranges between 24 in the river estuary areas and 35 in the offshore German waters. The study area is dominated by sandy and muddy-sandy sediments (Laurer et al., 2012). Muddy substrate occurs mainly in the Wadden flats and in the glacial valley of the Elbe River. In the shallower areas along the Elbe glacial valley, i.e. along the northern and eastern Frisian coast, sediments are patchy distributed with fine to coarse sand, gravel, cobble and stones. Temperature, sediment and depth are the most important environmental parameters shaping the spatial and temporal distribution of the macrofauna communities (Callaway et al., 2002; Van Hoey et al. 2004). The Dogger Bank, located at the tip of the German EEZ, represents a natural border between the deeper parts of the central North Sea and the shallower German Bight and therefore also acts as a transition zone of habitats dominated by southerly and northerly distributed species (Zettler et al., 2018).

The Belgian part of the North Sea

The Belgian part of the North Sea (BENS; 3600 km²) is the most south-western part of the Southern Bight of the North Sea and has a maximum depth of 46 m. This area is characterized by the presence of four isolated sandbank systems (Coastal Banks, Flemish Banks, Zeeland Banks and Hinder Banks) situated 10-30 km offshore, greatly contributing to the heterogeneity of the sea floor (Degraer et al., 2006). Sediments, and related benthic communities, in the BENS range from oxygen-stressed muddy sediments close to the shore to well oxygenized permeable, coarse sands and relatively small gravel beds further offshore (Braeckman et al., 2014; Montereale-Gavazzi et al., 2018; Breine et al., 2018). The offshore water column is composed of north-eastward flowing Atlantic water affected by freshwater discharges of several estuaries (rivers Seine, Somme, Scheldt and Rhine/Meuse (Lancelot et al., 1991; Yang, 1998; van Bennekom and Wetsesteijn, 1990), while the more near-shore waters are affected by freshwater outflows and residual gyre as a consequence of the discharge from the Western Scheldt river estuary (Arndt et al., 2011). The shallowness of the area, in combination with strong tidal currents results in a fully mixed water column (Simpson, 1994).

The Eastern English Channel

The English Channel (study area - 13927 km²) is a shallow epicontinental sea influenced by the Atlantic Ocean to the west and connected to the North Sea through the Dover Strait. Water masses may transit between the two marine areas, but only around 10 % of water that enters the North Sea flows via the English Channel, whereas the main outflow occurs through north-eastern open boundary. In the eastern

part of the Channel, tidal current strengths increase from 1.5 to 3 knots from the south to the northeast as the narrower part of the Dover Strait. Flow velocity decreases in the southern North Sea where it does not exceed 2 knots (S.H.O.M., 1968). Variations in the speed of the tidal current create a sedimentary gradient (Larsonneur et al., 1982). Pebbles and gravels prevail in the open sea, whereas coastal areas are dominated by large homogeneous sand banks and associated channel systems. The water quality is largely influenced by two main estuaries: the Seine estuary in the south-west, and the Scheldt delta in the north-east. Depending on the direction, intensity and duration of the wind, the plume of both rivers can reach the Dover Strait zone and modify the water salinity up to 2-3 miles off the French coasts (Brylinski et al., 1991). Other smaller rivers (i.e. Somme, Authie, Canche, Liane, Aa and Yser) and runoff from sea cliffs contribute locally to a decrease in the salinity of the coastal waters.

2.2. Macrofaunal data - sampling and processing

Temporal variability within the data differed between regions (Table 1), but all contributing datasets are largely constrained to recent data (starting from 1994). Though seasonal and interannual variation of BP_c is omnipresent, generally spatial variation in BP_c is significantly higher than temporal variation (see Supplementary material S1.2 and Gogina et al., 2017). The number of replicates and sieve size also deviated between sets, implying that comparisons between regions should be treated with caution.

Table 1 summarizes the different sampling strategies across the different regions. In DEBS, abundance and ash free dry weight biomass data were determined and averaged per station and standardised to the area of 1 m². A separate grab sample was taken at each sampling event for the determination of sediment characteristics (grain size analysis by sieving or laser particle size analysis and organic content by loss on ignition). In DENS, wet mass (g) was determined in the laboratory, and AFDW (ash-free dry weight in g) was calculated using the conversion factor database of Brey (2001). When multiple replicates (mostly one to three) were taken per station, data was averaged per station prior to the analysis. In BENS, biomass was measured as wet weight. When data were missing, mean individual wet weight values were used for recalculation. Wet weight biomass was converted to AFDW (g) using species-specific conversion factors from the in-house list of the Leibniz Institute for Baltic Sea Research, Warnemünde, or, for taxa not in the list, values from Ricciardi and Bourget (1998). If no conversion factor was available for a taxon, the conversion factor of the next higher taxon level was used. As the BENS benthic datasets were collected by two institutes (ILVO and Marine Biology Research Group of Ghent University), over different sampling campaigns and by different people with a varying level of expertise in sample handling and identification, data were subjected to an intense quality control (Breine et al., 2018). In ENCH, the biomass of each taxon

was determined in ash-free dry weight (AFDW, in g) per 0.5 m⁻², by calculating a loss of weight of dry organisms after 6h at 520°C. Although we are aware that a 2 mm sieve may cause difference in the results, we used this available dataset considering that more than 95% of the biomass (Ghertsos, 2002) and at least 83% of the biodiversity (Dethier and Berry, 2012) can be collected using such sieve mesh.

Table 1. Number of stations per sampling year, data set included in the study and related sampling strategy. DEBS = German part of the Baltic Sea; DENS = German part of the North Sea; BENS = Belgian part of the North Sea; ENCH = Eastern English Channel. Data sources: Leibniz Institute for Baltic Sea Research (DEBS), Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (DENS), ILVO and Marine Biology Research Group of Ghent University (BENS) and Ifremer (ENCH).

		DEBS	DENS	BENS	ENCH
Year	1994			45	
	1995			4	
	1996			7	
	1997		42	88	
	1998		5	49	
	1999	70	44	120	
	2000	72	214	72	
	2001	51	144	18	
	2002	119	110	71	
	2003	75	88	12	
	2004	118	42	105	
	2005	81	63	36	
	2006	78	113	223	85
	2007	128	15	192	8
	2008	10		285	
	2009	162		293	
	2010	167		309	
	2011	54	28	173	
	2012	102	56	114	
	2013	168	36		
	2014	153	59		
	2015	26			
	Total (incl. measured median grain size)	1634 (1115)	1059 (830)	2216 (1739)	93 (93)
Condit	Range of median sediment grain size, µm	6-4356	28-4000	12-770	160-920
	Range of depth, m	4.9-49.5	9.6-67.9	0-38.6	7.0-53.5

	Range of salinity	5.7-30.2	27.6-35.0	34.3-34.7	34.2-34.7
Strategy	Number of replicates per station	3	3	1	2
	Area sampled, m ²	0.1	0.1	0.1	0.25
	Main sampling gear (grab type)	Van Veen	Van Veen	Van Veen	Hamon ^a
	Sieve size, mm	1	1	1	2

a – 4 of 93 stations in ENCH were sampled with Rallier-du-baty dredge and were not included in modeling analysis

2.3. BP_c calculation

Bioturbation potential, used as proxy for benthic ecosystem functioning, was calculated (for each sampling event over the time spans covered by each data set) following the approach by Solan et al. (2004) with modifications described in Gogina et al. (2018):

$$BP_c = \sum_{i=1}^n BP_{pi}, \text{ where } BP_{pi} = (B_i/A_i)^{0.5} * A_i * M_i * R_i$$

where for taxon *i* *B_i* is biomass (in ash-free dry weight AFDW g m⁻²) and *A_i* is abundance (in ind. m⁻²) at each sample. *M_i*, mobility, and *R_i*, sediment reworking, are categorical scores assigned to each taxon based on ecological knowledge (*M_i*: 1 - living in a fixed tube, 2 - limited movement, 3 - slow, free movement through the sediment, 4 - free three dimensional movement via burrow system; *R_i*: 1 - epifauna that bioturbate at the sediment–water interface, 2 - surficial modifiers, 3 - upward and downward conveyors, 4 - biodiffusors, 5 - regenerators that excavate holes, transferring sediment at depth to the surface). The revised scores used for each taxon included in the analysis in each of the four regions (and thus the corresponding taxa lists) can be found in the Supplementary material S2. Values for species population bioturbation potential, *BP_{pi}*, summed across all taxa in a sample gives an estimate of community-level bioturbation potential, *BP_c*. The original *BP_c* equation (Solan et al., 2004) was adjusted by (i) using AFDW (instead of wet weight) biomass for the calculation, as it is often considered a better proxy for ecosystem functioning (e.g. Eklöf et al., 2017; Renz et al., 2018), and by (ii) totally excluding sedentary epifaunal species not involved in sediment transport from the calculation (i.e. species that scored 1 at both *M_i* and *R_i* were considered to have zero contribution to particle displacement in sediments).

2.4. Key species selection criteria

Key bioturbators were determined based on their contribution (i) to the cumulative total sum of *BP_c* across all stations in each region and (ii) to each unique station *BP_c* (similar to Gogina et al., 2017; Wrede et al., 2017). In DEBS overall 315 taxa contributed to bioturbation at 1634 sampling stations. 37 key species were

selected using the criteria of (i) at least 0.1% contribution to the cumulative total sum of BP_c across all stations or (ii) over 60% contribution to BP_c at a unique station and being recorded for at least 40 stations. In DENS, 33 of the 479 taxa recorded at 1059 stations contributed to (i) at least 0.6% of total sum of BP_c for all stations or (ii) over 50% at unique stations, and were found at more than 10 stations and were therefore selected as key species. For BENS 47 of 329 taxa recorded at 2216 stations were selected as key species using the criteria of contributing to (i) at least 0.5% of total sum of BP_c or (ii) over 50% of BP_c at unique stations and displaying at least 25 occurrences. In ENCH, 32 of 418 taxa recorded at 93 stations were selected as key species using the criteria of (i) at least 0.7% of total sum of BP_c for all stations or (ii) over 50% at unique station. The reasoning behind certain numerical deviations in selection criteria used across different regions was the intention to keep the number of selected key species per area relatively limited (below 50, feasible for calculation and processing/operability). Relevant for management perspectives, unlike in most studies here we highlight species important in terms of their contributions to bioturbation potential, i.e. functional contributions rather than biomass or abundance dominance.

To examine if functionally important species differ from those dominating the biomass we have also compared the top 10 species as computed by BP_c within and across regions relative to those computed from AFDW biomass.

2.5. Sediment classification

In order to harmonize sediment data, classification according to Wentworth (1922) was used for sampling events where median grain size data was available. The sediment classes (SedType) considered were: mud (M) $< 63 \mu m$, fine sand (FS) $63 - 250 \mu m$, medium sand (MS) $250 - 500 \mu m$, coarse sediment (CS) $\geq 500 \mu m$ (see the map in Supplementary material S1.1).

2.6. Abiotic predictors layers

A combination of physical, chemical, and biological components has a direct influence on the integrity of species and its habitats, thereby limiting the distribution of assemblages and its functional indicators (Reiss et al., 2015). To account for changes in abiotic drivers, for each of the 4 regions, we have collated available full-coverage environmental layers that were assumed relevant for ecological and physiological constraints and used these layers as predictors for spatial distribution modelling of BP_{pi} and BP_c . The sets for each region differed in number of predictor layers, origin, quality and resolution (Supplementary material S3).

General details on predictors for DEBS can be found in Gogina et al. (2017): sediment median grain size and bathymetry were obtained from Tauber (2012a) and Tauber (2012b); modelled euphotic depth and bottom detritus averaged over 2000 to 2010 – from Friedland et al. (2012) and Schernewski et al. (2015); porosity was estimated according to Endler et al. (2015); modelled near-bottom mean summer temperature, salinity (mean and standard deviation, SD), bottom shear stress, mean bottom currents velocity, oxygen concentration, number of anoxic days and concentration of suspended particulate matter (SPM), covering the period of 2001–2015, were based on Klingbeil et al. (2014) and Gräwe et al. (2015); layers on substrate fine fraction smaller than 63 μm , total organic content (TOC), N, P and mobile P (Leipe et al., 2017) were obtained from the Baltic Sea Atlas (<http://bio-50.io-warnemuende.de/secos>).

For the DENS layers for sediment median grain size, sorting parameter and mud fraction (< 63 μm) were obtained from point data originated from the Marine Environmental Data Base (MUDAB). Average and maximum bottom shear stress from currents and waves data was available for February 2006 (see e.g. Stanev et al. 2008). For the interpolation of median grain size and sorting inverse distance weighting method was used, whereas for mud the Natural-Neighbour method was applied. Water depth layer was obtained from Schlüter and Jerosch (2009). Temperature and salinity data were derived by the Estuarine Transport Model (Stips et al., 2004).

For the BENS, median grain size layer is obtained from Verfaillie et al. (2006) and Van Lancker et al. (2007), bathymetry and silt-clay sediment fraction layers are described in Van Lancker et al. (2007), details on Belgian Bathymetric Position Index (BPI, measure of location's position and elevation in relation to the overall landscape) can be found in Verfaillie et al. (2009), data on Suspended Particulate Matter (SPM) was obtained using the algorithm described in Nechad et al. (2009; 2010). Layers on tidal current and wave energy and light at seabed were obtained from EMODnet Seabed Habitats portal (<http://www.emodnet.eu/seabed-habitats>).

Details on predictor layers for ENCH, including bathymetry, bed shear stress, SPM, chlorophyll a and Particulate Organic Carbon (POC), sediment type, waves, Bathymetric Position Index (BPIbel) can be found in Foveau et al. (2017). Data on light at seabed and currents induced average kinetic energy (ke m^{-2}) at 1 m above the seabed were obtained from EMODnet. Near-bottom temperature and salinity (30 years average) refer to Núñez-Riboni and Akimova (2015).

2.7. Statistical analyses

To visualise the variation in relative contributions of taxa to BP_c on various sediment types and between regions we used non-metric multidimensional scaling (nMDS) superimposed by the results of the group

averaged Hierarchical Cluster analysis based on Bray–Curtis similarities. To test differences in the distribution of BP_c across sediment types (four levels, fixed factor) and regions (four levels, random factor) we have used two-way non-parametric permutational analysis of variance PERMANOVA (McArdle and Anderson, 2001; PRIMER 7 with PERMANOVA add-on), including the interaction between sediment type (SedType) and region. Unless stated otherwise, significance level of statistical tests was set to $p < 0.05$. In case of significance of the interaction term, pair-wise comparison was performed among SedType x region. PERMANOVA can be used to do univariate ANOVA based on permutations, thus avoiding the normality assumption, and is suitable for unbalanced data and heterogeneous dispersions among groups (Anderson, 2017).

PERMANOVA can be used to achieve partitioning for any additive model, but it is not particularly too sensitive to the differences in covariance structure, i.e. it does not care about the direction, but only about differences in dispersion (Anderson, 2017). Therefore, we have also assessed the trends of BP_c changes within each region along the gradients in median grain size and diversity (species richness). In particular, to check the overall relationship between BP_c , sediment properties (median grain size) and biodiversity (species richness), also accounting for the possible regional effects and covariance with salinity and depth we have fitted a linear regression in R (R Core Team, 2013). Subsequently, we have calculated the relative importance of each predictor in the fitted linear regression using the lmg metric (R^2 partitioned by averaging over orders) and package ‘relaimpo’ (Groemping, 2006). Kendall partial correlations were also checked prior to the analysis, using R package ‘ppcor’ (Kim, 2015) (Supplementary material S3).

For each region, we have also calculated the value of functional redundancy, defined as the difference between species diversity and Rao’s quadratic entropy based on the functional dissimilarity (de Bello et al., 2007), based on abundance and bioturbation traits, i.e. mobility and reworking scores.

2.8. Modelling approaches and estimates of predictive accuracy

There are several ways to obtain full coverage maps for BP_c . To test methods appropriate for different applications and evaluate differences in results across methods and regions, in this study we have used three of them. We applied a Random Forest machine learning algorithm (Breiman, 2001) that comprises an ensemble of randomly constructed decision trees, using the R package “RandomForest” (RF, Liaw and Wiener, 2002; R Core Team, 2013). Separately for each region, we employed two modelling approaches: i) where community bioturbation potential BP_c was initially the response variable (later referred to as “direct- BP_c ” approach), and ii) where a separate model (and map) was derived for bioturbation potential BP_p of each key species in the region as response variables, and resulting BP_p estimates were subsequently

summed together to derive an estimate of BP_c distribution (later referred to as “species-resolved” approach, see also Gogina et al., 2017). We have also generated BP_c maps using simple spatial interpolation by the natural neighbour method. The disadvantage of the last method relative to the proposed two modelling approaches is that fine-scale spatial differences between sampling locations are usually blurred, unless sampling density is sufficiently high (i.e. simple spatial interpolation methods are limited in including the variation of distribution driven by fine-scale habitat changes, see e.g. Franklin and Miller, 2010).

BP_c and BP_p values were $\log_{10}(x + 1)$ transformed prior entering the Random Forest models. We set the number of tree to 500 and we conducted a sensitivity analysis for the nodesize, i.e. the number of variables to be tested at each node, setting it from 1 to 5, and subsequently taking the best performing model (based on highest % of variance explained).

Prediction of BP_p for key species was based on the zero-inflated two-step procedure (Savage et al., 2015). First, presence/absence of considered species was predicted for each cell using binary classification RF. Second, only non-zero reference data was utilized to train a continuous RF regression model. The final region-wide prediction for each BP_p was produced by combining the binary classification map with a continuous map: zero values were assigned to any cell predicted as absence; for cells that were identified as presence in the first step, the values from the second-step continuous prediction were assigned.

To estimate predictive accuracy of each modelling approach and compare them we used the non-parametric Kendall's τ rank correlation between BP_c values based on observed macrofauna data and those resulted from Random Forest models. Modelling results were also compared with the results of natural neighbour spatial interpolation driven only by the input samples. This interpolation finds the closest subset of input samples to a query point and applies weights to them based on proportionate areas to interpolate a value. For the ENCH region, a comparatively low sample size (93 stations) was available. This raised the concern that the continuous models would provide poor predictive accuracy (e.g. negative % of variance explained, indicating that it is better to simply predict any sample as equal to grand mean than using the given model) for species having lower frequency of occurrence. The “% of variance explained” value was higher when the zero-inflation step was omitted. However, comparison of model results with observed data showed that the employment of the zero-inflated two-step method produced an overall more accurate prediction results. For the example for *Galathea intermedia*, Kendall's τ correlation between observed and predicted BP_p values were 0.85 and 0.52 with and without zero-inflation step,

respectively. In case of BENS all RF modelling and spatial interpolation processing was additionally done on BP_c values aggregated per 1km grid cell in order to level out temporal fluctuations.

We have grouped all predictors into nine larger categories according to the parameters they describe (sediment properties, food availability, oxygen conditions, salinity, exposure to currents (that can also be referred to as oceanographic stress), light conditions, temperature, depth, and human pressure, see Supplementary material S3) as the predictor layers differed between regions, to allow cross-comparisons of environmental drivers across regions. Subsequently, the importance of categories of environmental predictors in explaining the spatial distribution of BP_c in the final models derived for each region was compared based on the values of the %IncMSE (the increase in mean squared error of predictions as a result of variable j being permuted, i.e. values randomly shuffled, estimated with the out-of-cross-validation), its corresponding maximum value per category, and its rank within all the predictors used in the final model per region.

2.9. Simplified application example

Regionally-derived BP_c maps for each area can be converted to benthic ecosystem functioning maps, applicable for management purposes, as BP_c may serve as proxy for estimates of spatial distribution of geochemical fluxes and nutrient cycling (Snelgrove et al., 2014; Gogina et al., 2018).

To illustrate the possible application of our proposed models we have estimated the spatial distribution of denitrification rates as function of BP_c in the BENS region based on the significant regression reported in Braeckman et al. (2014): $\text{Denitrification} = 0.68 + 0.004 \cdot BP_c - 3.00e^{-07} \cdot BP_c^2$. It is important to note that in Braeckman et al. (2014) WW biomass was used to calculate BP_c . To solve this for our (simplified qualitative rather than quantitative) example, we applied the linear regression to convert AFDW-based BP_c to WW-based BP_c . If the resulting estimates were negative (unphysical) they were set to zero, as was suggested by Braeckman et al. (2014).

As the “species-resolved” modelling approach used here provides the information resolved to key species (BP_p) level, the possible further application for it is testing the scenarios for key species loss or gain, i.e. an assessment of impact expected for ecosystem functioning when these species are subjected to anthropogenic pressures. For this purpose, we have removed the contributions of 14 randomly selected key taxa (30% of the contributing taxa) from BP_c estimates by the “species-resolved” approach to assess the possible functional effect of structural biodiversity loss.

3. Results

3.1. Key species

The summed BP_p for the selected species was responsible for over 90% of total BP_c in DEBS and BENS, 87% in DENS and slightly over 73% in ENCH (Supplementary material S4). Top five species contributing most for each sediment type (mud, fine, medium or coarse sand) in each region are listed in Table 2.

Generally, some dominant (here and below in this section – dominant in terms of the contribution to BP_c) species were shared by all considered sediment types in the particular regions (such as *Hediste diversicolor* in DEBS or *Echinocardium cordatum* in both DENS and in ENCH). Concurrently, several taxa (including *E. cordatum*, *Branchiostoma lanceolatum*, *Ensis leei* or *Nephtys* spp.) appeared through several regions with some shift between the sediment types. For instance according to nMDS and Hierarchical Cluster analysis on relative BP_{pi} , top contributors for coarse sand in ENCH were closer to medium and coarse sands in the DENS than to taxa listed for finer sediments of ENCH (see Figure 1). In all four regions the highest contribution of five top-most bioturbating taxa was found in fine sands.

In the DEBS, *Hediste diversicolor* had the overall highest contributions to total BP_c in mud, medium and coarse sands (with respective contributions declining from 23 to 15%). It was also listed 3rd for fine sand, preceded by *Arctica islandica* and *Peringia ulvae*, with three species together sharing over 32% of total contribution in fine sands. In medium sand *H. diversicolor* and *A. islandica* accounted for 39% total BP_c . All shortlisted species were either surficial modifiers or biodiffusors. *Limecola balthica*, *Diastylis rathkei* and *Nephtys ciliata* were shortlisted only for muddy stations; *Tubificoides benedii* and *Tubificidae* - only for coarse sands.

For muddy sediments of DENS, *Amphiura filiformis*, *Nucula nitidosa* and *Nephtys hombergii* together accounted for nearly 67% of total BP_c . *Amphiura filiformis* also had marked contribution in fine and medium sands. *Echinocardium cordatum* was most dominant in fine sands, but was shortlisted for all 4 sediment types and responsible for over 25 % of total BP_c in the region. *Branchiostoma lanceolatum* had the highest contribution in medium and coarse sands; *Ophelia borealis* and *Nephtys caeca* were also listed among top 5 for these two sediment types. Most of listed species were attributed to slowly free moving biodiffusors; *Ensis leei* (listed only for mud) was a single shortlisted surficial modifier.

At the muddy stations of BENS *Abra alba*, *Notomastus latericeus* and *Anthozoa* together accounted for over 50% of total BP_c , whereas *E. leei* and *A. alba* shared over 40% of total contribution in fine sands. In contrast to the DENS, *Nephtys cirrosa* had the highest contribution in medium and coarse sands; *E.*

cordatum was listed only for those two sediment types. For medium sand stations it was followed by *E. leei*, for coarse sands - *Branchiostoma lanceolatum* and *O. borealis* had higher contributions.

In the ENCH again *E. cordatum* was the most important bioturbator at fine sand stations (as well as among all stations included in the analysis), followed by *N. cirrosa* and *O. borealis*. *N. cirrosa* and *Ophiothrix fragilis* contributed most in medium sands. *B. lanceolatum*, listed fifth for medium sands, was on the first place in coarse sands.

Remarkably, there are species that are within the top 5 across all sediment types within a region, e.g. *Hediste diversicolor* in DEBS, as well as species that are in within the top 5 for a specific sediment type across regions, e.g. *B. lanceolatum* and *O. borealis* in coarse sand across 3 of the four regions. This can help to point out species that might be important to protect or manage, but which are often neglected in management plans.

Table 2. Top five key taxa listed per sediment type per each region. The values for species contribution (in %) to the total BP_c at all stations considered for each region indirectly indicates the dominance of the particular sediment type in the area. Also the percent of total BP_c at all stations covering specific sediment type, and mobility (*M*) and reworking (*R*) scores attributed to each taxon (indicated by the first and the second digit, correspondingly; for meaning of scores refer to section 2.3) are indicated.

Sediment type	DEBS				DENS				BENS				ENCH			
	Taxa	% of total	% of total per SedType	MR scores	Taxa	% of total	% of total per SedType	MR scores	Taxa	% of total	% of total per SedType	MR scores	Taxa	% of total	% of total per SedType	MR scores
Mud M	<i>Hediste diversicolor</i>	2.1	23.4	44	<i>Amphiura filiformis</i>	2.2	48.9	34	<i>Abra alba</i>	0.05	23.5	22				
	<i>Arctica islandica</i>	1.8	1.7	22	<i>Nucula nitidosa</i>	0.6	13.1	32	<i>Notomastus latericeus</i>	0.04	19.0	23				
	<i>Nephtys ciliata</i>	0.8	0.2	34	<i>Nephtys hombergii</i>	0.2	4.9	34	<i>Anthozoa</i>	0.02	11.7	22				
	<i>Diastylis rathkei</i>	0.7	0.9	32	<i>Echinocardium cordatum</i>	0.2	4.9	34	<i>Eunereis longissima</i>	0.02	9.8	44				
	<i>Limecola balthica</i>	0.7	2.7	22	<i>Ensis leei</i>	0.1	3.0	22	<i>Cirratulidae</i>	0.02	7.8	22				
	Sum	6.1	28.9		Sum	3.3	74.7		Sum	0.2	71.8					
Fine sand FS	<i>Arctica islandica</i>	4.0	12.3	22	<i>Echinocardium cordatum</i>	25.4	31.4	34	<i>Ensis leei</i>	24.2	33.9	22	<i>E. cordatum</i>	9.3	27.6	34
	<i>Peringia ulvae</i>	3.8	11.6	32	<i>Amphiura filiformis</i>	18.1	22.4	34	<i>Abra alba</i>	5.4	7.6	22	<i>Nephtys cirrosa</i>	4.1	12.2	34
	<i>Hediste diversicolor</i>	2.7	8.3	44	<i>Nemertea</i>	3.7	4.5	34	<i>Lanice conchilega</i>	4.5	6.3	13	<i>Ophelia borealis</i>	1.8	5.4	34
	<i>Mya arenaria</i>	2.4	7.3	22	<i>Spiophanes bombyx</i>	2.3	2.9	13	<i>Owenia fusiformis</i>	4.4	6.1	12	<i>Ophiothrix fragilis</i>	1.4	4.2	22
	<i>Scoloplos armiger</i>	2.4	7.3	34	<i>Nephtys hombergii</i>	2.1	2.6	34	<i>Nephtys hombergii</i>	3.3	4.6	34	<i>Scoloplos armiger</i>	0.9	2.6	34
	Sum	15.3	46.8		Sum	51.6	63.7		Sum	41.8	58.5		Sum	17.6	52.0	
Medium sand MS	<i>Hediste diversicolor</i>	2.4	21.3	44	<i>Branchiostoma lanceolatum</i>	1.2	15.5	34	<i>Nephtys cirrosa</i>	3.0	22.6	34	<i>Nephtys cirrosa</i>	4.2	9.8	34
	<i>Peringia ulvae</i>	1.4	1.7	32	<i>Amphiura filiformis</i>	0.9	11.6	34	<i>Echinocardium cordatum</i>	1.9	14.3	34	<i>Ophiothrix fragilis</i>	3.3	7.7	22
	<i>Astarte borealis</i>	1.2	1.1	22	<i>Echinocardium cordatum</i>	0.8	10.5	34	<i>Ensis leei</i>	1.3	9.5	22	<i>Echinocyamus pusillus</i>	2.4	5.7	32
	<i>Arctica islandica</i>	1.1	17.7	22	<i>Ophelia borealis</i>	0.7	9.2	34	<i>Ophelia borealis</i>	0.5	3.8	34	<i>Ophelia borealis</i>	2.3	5.5	34
	<i>Scoloplos armiger</i>	0.9	5.5	34	<i>Nephtys caeca</i>	0.3	3.7	34	<i>Anthozoa</i>	0.5	3.5	22	<i>B. lanceolatum</i>	1.9	4.4	34
	Sum	7.0	47.3		Sum	4.1	50.5		Sum	7.1	53.8		Sum	14.1	33.2	
Coarse sand CS	<i>Hediste diversicolor</i>	1.8	15.4	44	<i>Branchiostoma lanceolatum</i>	3.4	53.2	34	<i>Nephtys cirrosa</i>	0.1	28.6	34	<i>B. lanceolatum</i>	3.7	8.7	34
	<i>Tubificoides benedii</i>	0.5	2.8	34	<i>Echinocardium cordatum</i>	0.3	4.5	34	<i>Ophelia borealis</i>	0.04	9.7	34	<i>Glycymeris glycymeris</i>	1.8	4.3	22
	<i>Tubificidae</i>	0.5	2.4	34	<i>Ophelia borealis</i>	0.3	4.2	34	<i>B. lanceolatum</i>	0.03	6.2	34	<i>E. cordatum</i>	1.1	2.5	34
	<i>Peringia ulvae</i>	0.4	8.7	32	<i>Orbinia</i>	0.2	3.2	34	<i>Echinocardium cordatum</i>	0.02	5.5	34	<i>Glycera lapidum</i>	1.0	2.4	34
	<i>Astarte borealis</i>	0.4	7.3	22	<i>Nephtys caeca</i>	0.2	2.6	34	<i>Oligochaeta</i>	0.02	4.1	34	<i>Glycinde nordmanni</i>	0.8	1.9	34
	Sum	3.6	36.6		Sum	4.3	67.8		Sum	0.2	54.1		Sum	8.5	19.9	

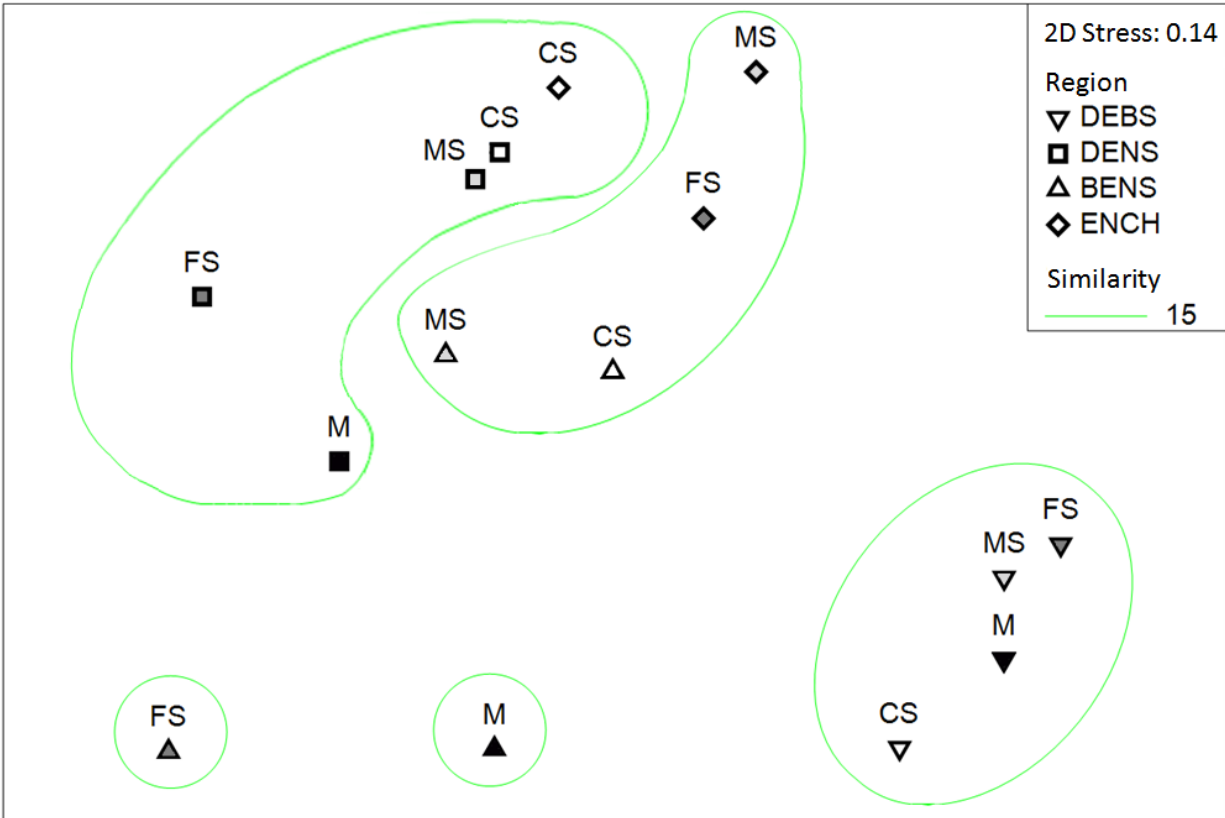


Fig. 1. Non-metric multidimensional scaling ordination plot of Bray-Curtis similarities based on square-root transformed species contributions to BP_c (relative BP_{pi}) in 4 sediment types at each region. Labels (and colour of the symbols) indicate sediment type (see section 2.5 for abbreviations), shapes of the symbols indicate different regions. Contours indicate the 15% Bray-Curtis similarities cut-off according to Hierarchical Cluster analysis (group average) to visually highlight differences.

The comparison of top 10 species as computed by BP_c within (see Supplementary material S1.3) and across regions (see Table 3) relative to those computed from AFDW biomass showed that: (i) there are regional differences, (ii) 4 species appeared in both lists and comprised > 20 % of both total BP_c and total AFDW biomass across the 4 regions, and (iii) there is also a mismatch between those that are functionally important and those that dominate biomass, for the reason that biomass as a metric does not account for what species with that biomass do.

Table 3. Top 10 key taxa contributing to total BP_c and AFDW biomass across all 4 regions. Taxa indicated in bold font appear in both lists (i.e. dominate both BP_c and AFDW biomass).

Taxa	% of total BP _c	Taxa	% of total AFDW biomass
<i>Echinocardium cordatum</i>	11.4%	<i>Echinocardium cordatum</i>	12.6%
<i>Ensis leei</i>	6.6%	<i>Arctica islandica</i>	10.5%
<i>Amphiura filiformis</i>	5.3%	<i>Ensis leei</i>	8.5%
<i>Nephtys cirrosa</i>	4.5%	<i>Lanice conchilega</i>	6.3%
<i>Hediste diversicolor</i>	2.8%	<i>Arcopagia crassa</i>	5.8%
<i>Branchiostoma lanceolatum</i>	2.7%	<i>Mytilus edulis</i>	3.9%
<i>Scoloplos armiger</i>	2.7%	<i>Amphiura filiformis</i>	3.2%
<i>Limecola balthica</i>	2.5%	<i>Laevicardium crassum</i>	3.2%
<i>Peringia ulvae</i>	2.4%	<i>Glycymeris glycymeris</i>	2.3%
<i>Arctica islandica</i>	2.2%	<i>Mya arenaria</i>	2.2%
Sum	43.1%	Sum	58.4%

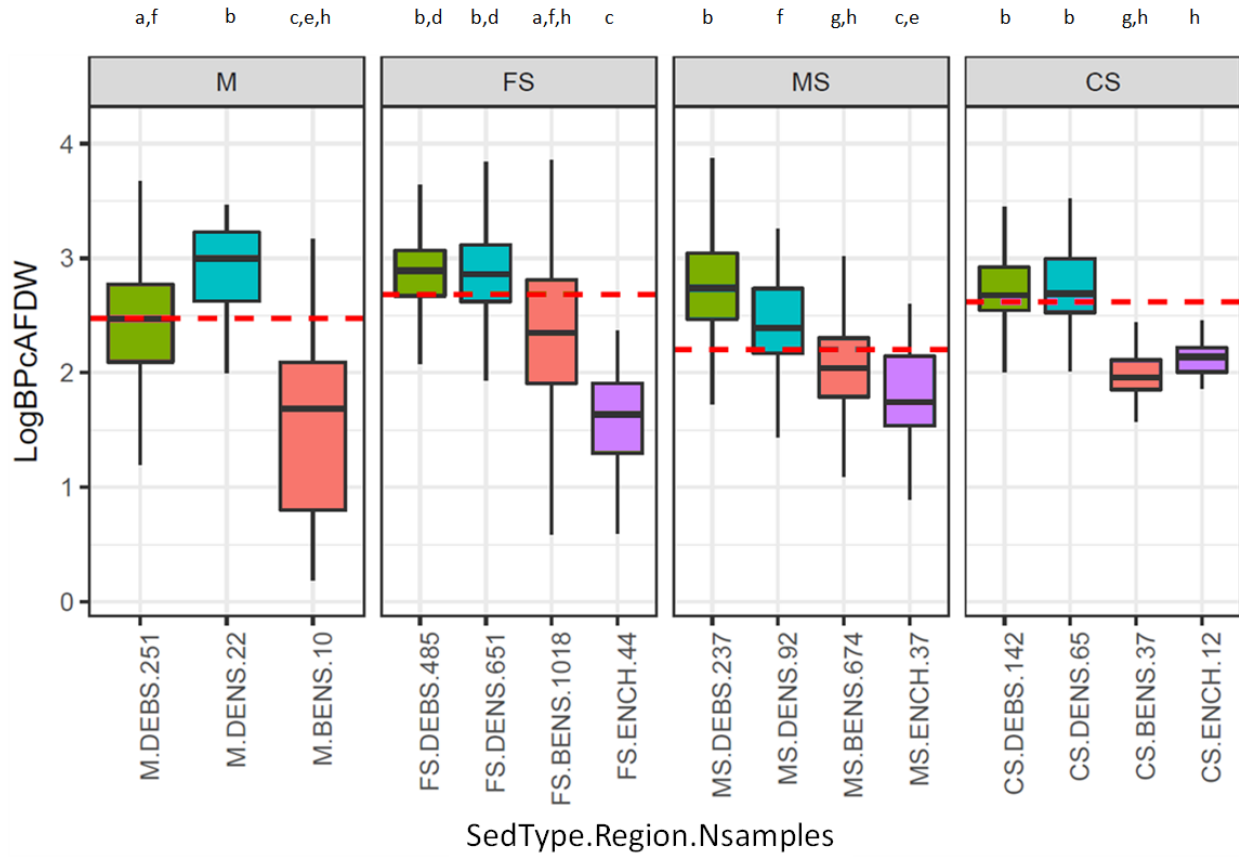
3.2. Differences in bioturbation potential between sediment types and regions

The effect of sediment type on BP_c was regionally dependent (two-way PERMANOVA Region x SedType interaction term: P(permanova) < 0.05; see Supplementary material S5).

Results of pairwise tests (Fig. 2A) indicated that similar magnitudes of the BP_c occur in DEBS and DENS for coarse and fine sand, and between BENS and ENCH for coarse sand (Fig. 2A). In DEBS no significant difference in BP_c values was found between fine, medium and coarse sand, where BP_c was higher than in muddy sediments. In DENS BP_c values in medium sand were significantly lower than records for mud, fine or coarse sand. In the BENS highest variability and therewith highest overlap was observed for all sediment type subsets, hence, no significant difference in BP_c values between the different sediment types were found. BP_c values for the ENCH were significantly lower in fine and medium sand compared to those in coarse sand.

Generally, lowest median BP_c values were recorded in ENCH, and BP_c in BENS was lower than in DEBS and DENS as well (Fig. 2B). Concurrently, there was a slight increase of calculated median values of functional redundancy observed from DEBS to ENCH (Supplementary material S5).

A



B

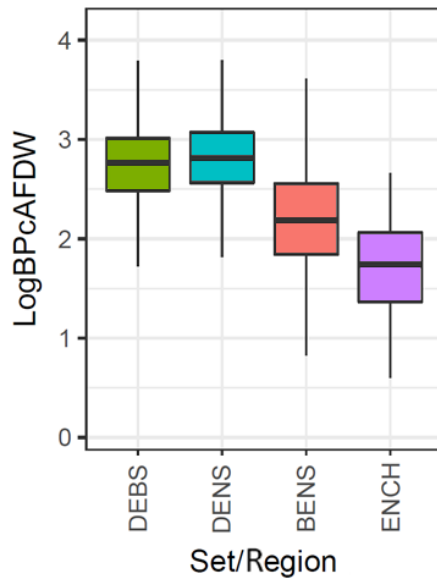


Fig. 2. Boxplots showing (A) regional differences in BP_c between different sediment types (M, FS, MS and CS are mud, fine sand, medium sand and coarse sediment, respectively, see Section 2.5; colour-coded are different regions). Numbers in the labels indicate the number of stations included in each subset. Dashed

red line indicates the median BP_c level per sediment type. Subsets sharing the same letter above the plots are not significantly different (based on pairwise tests within PERMANOVA). (B) Differences in BP_c between different regions. Whiskers span from the bottom 5% to the upper 95%, boxes span from 25% to 75%.

3.3. Spatial distribution

Results of modelling and interpolation of spatial distribution of BP_c are shown in Figure 3, for DEBS, DENS, BENS and ENCH, respectively. Generally, Kendall's τ values (calculated to evaluate method performance) were highest for the simple spatial interpolation approach for all the regions, confirming its closest association with observations. Furthermore, Kendall's τ values for RF modelling using BP_c as response (“direct- BP_c ” approach; Fig. 3A) were always higher than those corresponding to the “species-resolved” modelling approach based on the summation of BP_p 's for key species (Fig. 3B).

In our “direct- BP_c ” modelling approach using BP_c as response variable in RF models, the final models explained 51.37% of the total variance of BP_c in the DEBS, 37.21% in the DENS, 36.9% in the BENS and 28.22% in the ENCH region (Supplementary material S4). The resulting maps for each region are shown in Figs. 3A. Maps resulting from the “species-resolved” approach predicted by an ensemble of RF models are shown in Figs. 3B. The variance explained by species-specific models BP_p models for key species ranged greatly, from 69.6% for both *Bathyporeia pilosa* in DEBS and *Amphiura filiformis* in DENS to only noise fitted (negative value of variance explained by continuous model) for many key taxa like *Nephasoma minutum* in the ENCH (see Supplementary material S4).

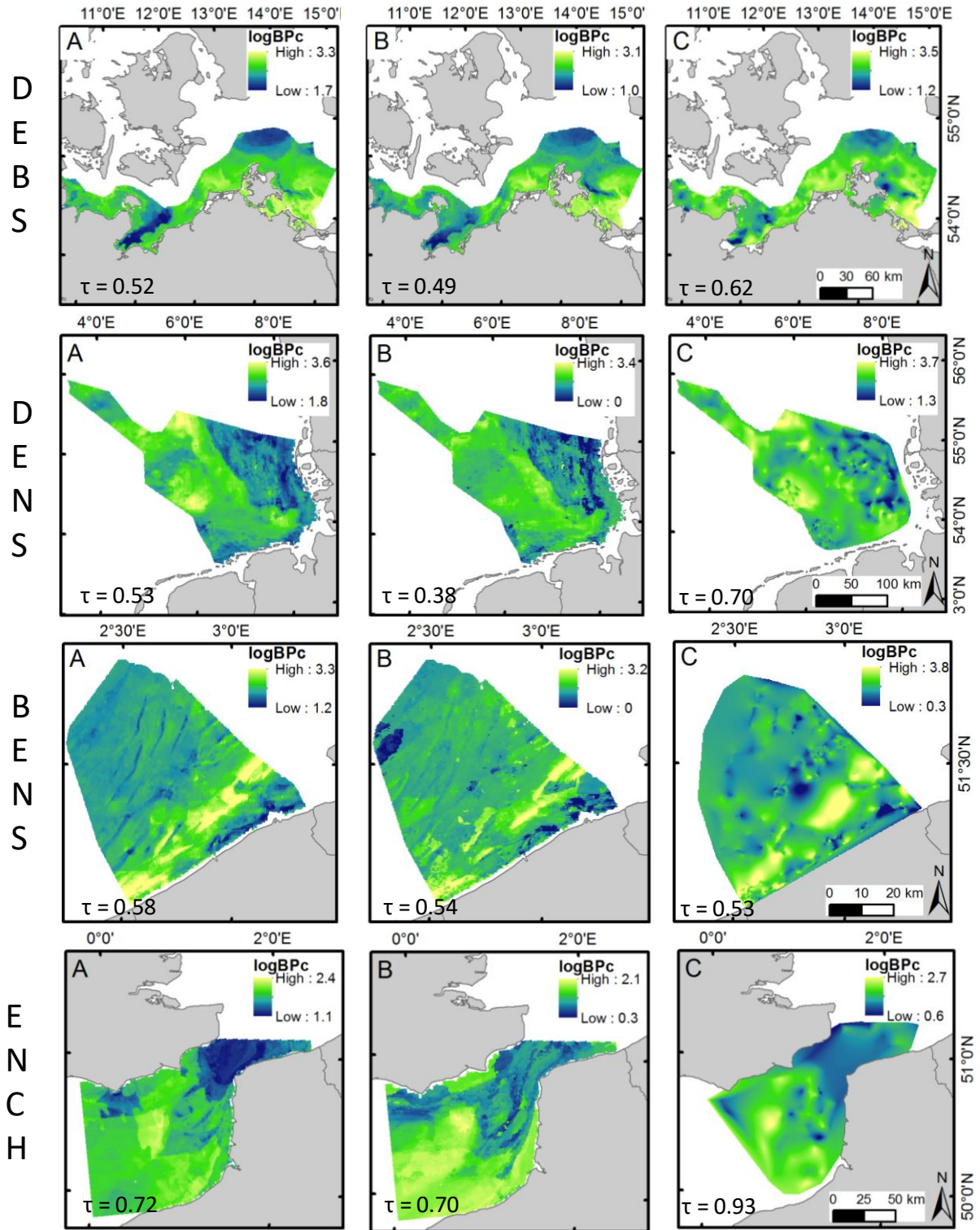


Fig. 3. Predicted surfaces of spatial distribution of BP_c (log-transformed values) in the different regions (A) direct RF modelling of BP_c as response variable (“direct- BP_c ” approach), (B) summation of BP_p ’s predicted by an ensemble of RF models for key species (“species-resolved” approach), and (C) natural neighbour

interpolation results (iii approach; Projection: WGS_1989_UTM_Zone_32N). Kendall's τ with observed values are reported on each figure ($p < 0.05$).

Based on the “direct- BP_c ” modelling approach, BP_c values in DEBS were mainly linked to sediment properties (i.e. median grain size and porosity), followed by food availability (sediment organic content and SPM), oxygen conditions and salinity (Table 4, Supplementary material S3). In DENS sediment properties, followed by exposure to currents (bottom shear stress due to waves), bottom temperature and human pressure (namely trawling frequency) affected BP_c values most. In BENS bathymetry, sediment properties (% of silt and clay in sediments) and current energy were the most important drivers. In ENCH these were current energy, bottom temperature and salinity.

The average rank of most important predictors for the “species-resolved” modelling approach differed from the main drivers listed above for the “direct- BP_c ” approach. This was expected, as for the entire assembly of species-specific BP_p models, the most important predictors can only be extracted by averaging the ranks of predictors ranks for each species. Thus it reflects an average combination of environmental preferences and sensitivity of selected key taxa listed for each region (Supplementary material S2 and S3). In DEBS these drivers were depth, salinity and light conditions. In DENS, sediment properties (median grain size), exposure to currents (kinetic energy at the bottom) and bottom temperature were most important in driving most of the species-specific BP_p models. In BENS food availability (particular organic carbon and SPM), bottom salinity, temperature and depth were the most important predictors in a set of models predicting species-specific BP_p . In the ENCH, again food availability (particular organic carbon), bottom temperature and salinity were often the most important predictors in the “species-resolved” approach.

Table 4. The importance of different categories of environmental predictors in explaining the spatial distribution of BP_c in the final models derived for each region (using “direct- BP_c ” approach). Values correspond to the maximum %IncMSE per category. The colour intensity of each cell inversely corresponds to the rank of the group of predictors per regions (i.e. from most important category of predictors in dark red to least important in grey), whereas white cells indicate that predictors of the category were not available for the corresponding region.

	DEBS	DENS	BENS	ENCH
sediment_properties	30.4	19.6	37.3	8.4
food_availability	29.3	13.6	35.2	
oxygen_conditions	26.4			
salinity	25	11.4	30.4	16.9
exposure_to_currents	24.9	14.4	36.7	24.4
light	24.1	2.6	34	
temperature	22.8	13.9	34.4	18.9
depth	21	10	39.4	12
human		14		

3.4. Effects of sediment grain size and biodiversity

When treating data from all regions together, BP_c was stronger, and positively, associated with biodiversity (species richness) than with median sediment grain size (Fig. 4 and Supplementary Material S5). Linear regression analysis suggests that BP_c value in DEBS were higher than in other regions, for stations having similar species richness and median grain size (and also controlling for weak effects of salinity and depth). Associations of BP_c with median grain size vary in the direction between regions, but were overall weak (Supplementary Material S5). Relative importance of factors driving the overall patterns of BP_c assessed using lmg metric (Table 5) was highest for species richness and region, followed by their interaction and salinity, whereas the effects of depth and median grain size were marginal.

A large variation of BP_c occurs along sediments similar in grain size (Fig. 4A). Difference in fitted region-specific trend lines highlights that the relationship between BP_c and sediment type differs between

regions. Moreover, a large range of BP_c occurs even along the low species richness values (Fig. 4B), suggesting that provisioning of high bioturbation activity is possible also under low diversity but high abundance and biomass, respectively.

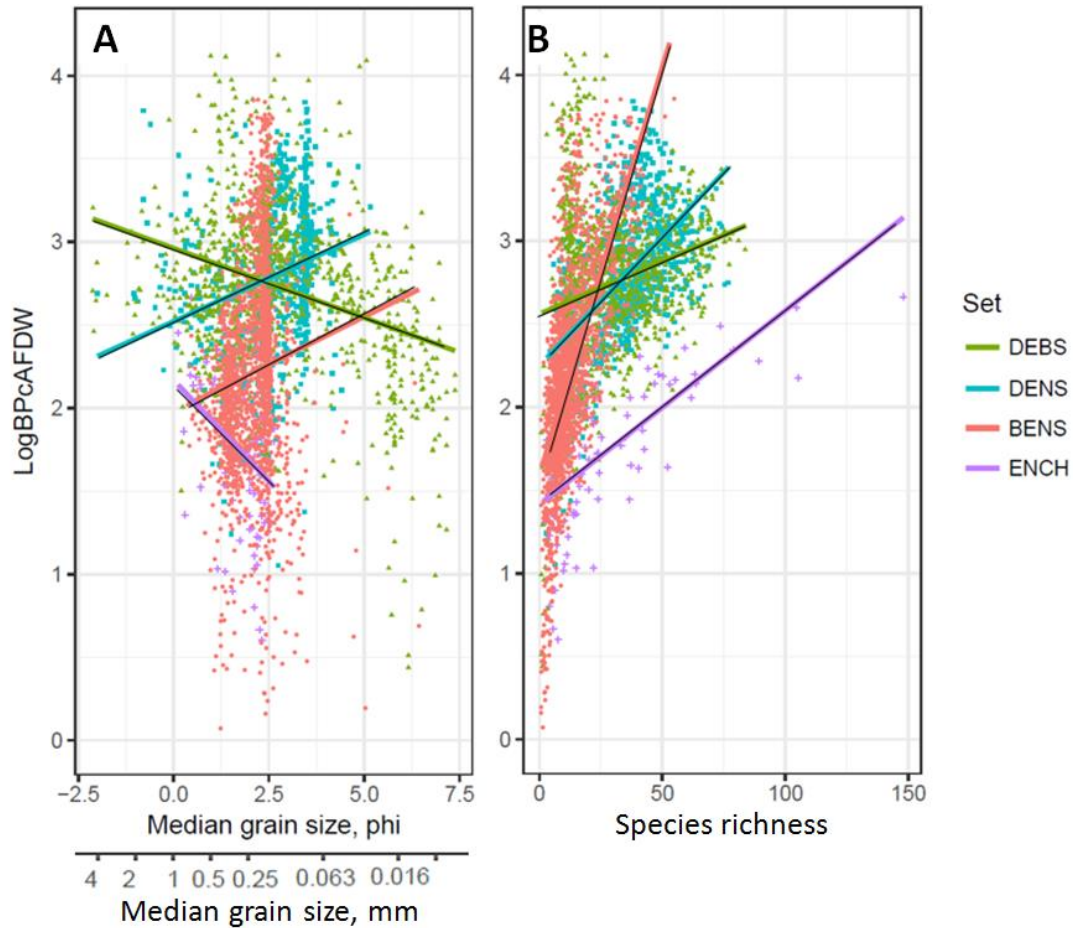


Fig. 4. Scatter plot of BP_c (log-transformed values) in each region against (A) median grain size and (B) species richness. The simple region-specific trend lines are fitted by generalized linear models to illustrate general patterns (see also Supplementary Material S5.4). Note that the slope should not be compared between regions as the sieve size and number of replicates deviated between regions.

Table 5. Relative importance of (groups of) regressors based on the lmg metric, including interactions.

Regressor/group	lmg	lmg normalized
Number of species	0.216	0.390
Median grain size, mm	0.004	0.006
Region (group of 3 regressors)	0.159	0.288
Depth, m	0.025	0.045
Salinity	0.032	0.058
Median grain size : Region	0.007	0.013
Number of species : Region	0.110	0.200

3.5. Application example – simplified estimate of species loss effect for denitrification in BENS

The resulting estimated distribution of denitrification in BENS, calculated as function of BP_c , is shown in Fig. 5. The removed species accounted together for 16% of BP_c in the area (with *Nephtys hombergii* and *Scoloplos armiger* having the highest contributions to BP_c of 7 and 5%, respectively).

The resulting predictions suggested highest rates of denitrification occurring in the fine sandy sediments south off the Flemish Banks and in the central and western coastal area. The “species-resolved” approach generally underestimates denitrification relative to the results obtained using “direct- BP_c ” approach (Fig. 5A-5C).

Overall lowest denitrification rates occur further offshore in the permeable sediments in the northern parts of the area and in the muddy sediments near the Western Scheldt estuary, where also the highest (over 50%) relative reduction of denitrification is predicted by the “species-resolved” approach under the tested theoretical scenario of biodiversity loss (Fig. 5D-5E).

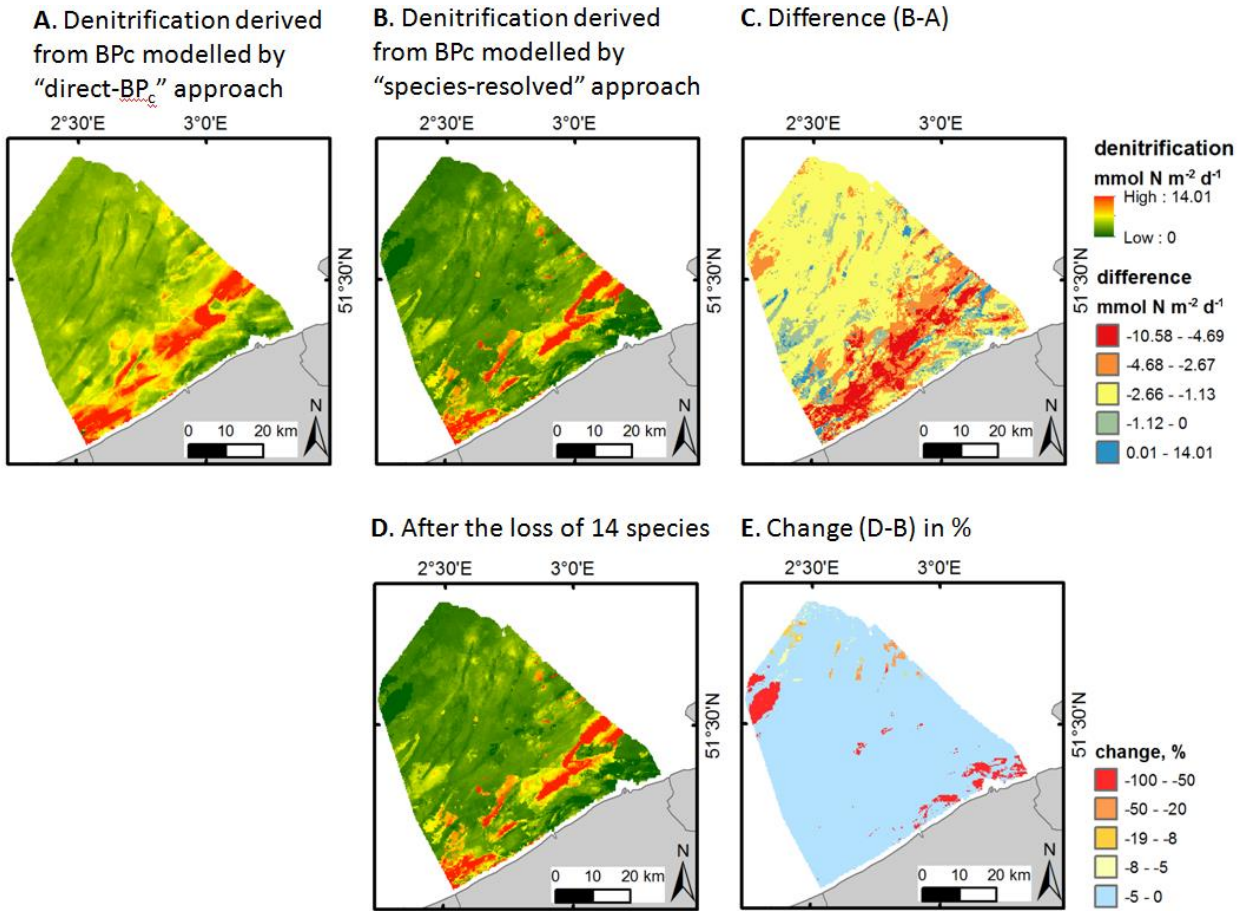


Fig. 5. Estimated denitrification in mmol N m⁻² d⁻¹ in BENS calculated (based on the findings of Braeckman et al. 2014) as function of BP_c (A) modelled by “direct-BP_c” approach, (B) modelled by second approach accounting for all key species, and (D) using “species-resolved” approach after the loss of 14 random species. The deviations of the denitrification estimates based on BP_c derived by two modelling approaches (C) and the potential changes of denitrification rates caused by species loss (E).

4. Discussion

Marine ecosystems are experiencing rapid and pervasive changes in biodiversity and species composition. Understanding the consequences of these changes for ecosystem functioning and assessing biodiversity-ecosystem functioning relationships is critical to effectively manage these systems (Gamfeldt et al., 2015; Strong et al., 2015; Birchenough et al., 2015; Zeppilli et al., 2016). Instead of focussing on species restoration only, sustainable management should also focus on ecological functions that support ecosystem services important for humanity. Bioturbation is one important ecological function of marine

benthos that is often associated with enhanced nutrient cycling in and from sediments (Gamfeldt et al. 2015). Therefore, studies addressing large scale bioturbation patterns in macrobenthic communities are urgently needed in order to assess dedicated processes and functions across these areas. In this study we identified for the first time the region and sediment-specific key species contributing to BP_c , over 4 distinctive regions along the European Shelf. We analysed regional patterns and drivers by modelling the spatial distribution of BP_c , and generated BP_c maps that can highlight hot-spots of benthic ecosystem functioning, which should be considered in the context of conservation goals and marine management.

4.1. Key species

In each region we observed a similar pattern of a few species contributing strongly to bioturbation, whereas other species contributed very little (Supplementary material S1.3, Supplementary material S4). Interestingly, very few key species occurred across multiple regions. However, if they were found in multiple regions, their contribution to BP_c was high in one region and small in the other. This suggests the overall importance of functional redundancy in communities (see Supplementary material S5.3 and the discussion below).

Similar to the results of Solan et al. (2012) for the North Sea, the contributions of key functionally important species varied tremendously between locations and regions; in this study, specifically, substantial differences were also revealed depending on selection procedure, i.e. based on AFDW biomass or contribution to BP_c . Across all 4 regions, there were four species that appear to be particularly important both functionally and in terms of biomass - *Echinocardium cordatum*, *Ensis leei*, *Amphiura filiformis*, *Arctica islandica* – where the first three species are mainly present in the North Sea, while the last one is important in the Baltic Sea. Species that were selected both via BP_c and AFDW reflect the fact that BP_{pi} is indeed partly influenced by biomass. However, there was also a mismatch between functionally important species (in terms of BP_c) and those that dominated biomass, reflecting the importance of differences in species behaviour (Hale et al., 2014).

4.2. General and regional patterns

Bioturbation may be thought as the result of reworking of sediment by the different species as they dig into the sediment for feeding or hiding from predators. Therefore, bioturbation is a combination of local properties (i.e., more related with the ecological features of the species causing it) and large-scale properties (i.e., related with broader environmental conditions; Gray and Elliott, 2009). The comparison between the regions in our study allowed us to highlight the gradient from areas fully driven by local-scale conditions (DEBS) to areas fully driven by broad-scale environmental conditions (e.g., ENCH). For instance

in DEBS bioturbation was mostly driven by sediment type and food availability, whereas in ENCH bioturbation was mostly driven by exposure, temperature and salinity. Regions between these two extremes, i.e. DENS and BENS had mixed conditions of drivers acting at local spatial scale (e.g., sediment type) and those acting at broad spatial scale (e.g., exposure; for definition of spatial scales see Pittman, 2017). We think that the slight trend of increase in calculated values of functional redundancy (Supplementary material S5.3) observed from the DEBS to the ENCH matches the trend of conditions from the local-scale (in DEBS) to broad-scale (in ENCH). In fact, drivers acting at local scale may support a higher heterogeneity of habitat and communities and therefore a wider range of functional redundancy. In turn, drivers acting at broad scales may support a narrower span of functional redundancy.

The remarkable decrease of BP_c from low-saline and species poor Baltic Sea towards the southern part of the North Sea (Fig. 2) appeal for more regional investigations (but see Gogina et al., 2017, Wrede et al., 2017). This phenomenon perhaps is also inversely related to functional redundancy (Supplementary material S5.3), that is expected to be lowest in the species poor areas where few (sometimes large) species with high dominance (Supplementary material S5.2) can potentially translate in increased levels of ecosystem functioning (as for example in case of *Arctica islandica*, *Mya arenaria* and *Hediste diversicolor* in DEBS). Conceivably, this reflects an effect of the mathematical formulation of BP_c (see Section 2.3) that results in higher inflation when a large number of lower scaled values is summed together compared to the sum of a lower number of high values. More precisely, the scaling factor 0.5, used in BP_c in this study, puts relatively more weight on species with low body mass and high abundance (like *Peringia ulvae*), which might in turn cause a potential bias towards Baltic Sea specimens that tend to be smaller (Supplementary material S1.3 and S5.2). Both mobility and reworking mode scores weighted by abundance tend to be higher in the Baltic Sea and decline towards ENCH (Table 2). Furthermore, the reduction of BP_c index towards the lower latitudes within the investigated dataset must be sought in the reduction in biomass and abundance per area. Such pattern can be observed in previous works that studied the global distribution of those metrics of biodiversity, e.g. Wei et al. (2010). The distribution of abundance and biomass values compared between regions (see boxplots in Supplementary material S5), suggest that both major community parameters are important in shaping the patterns of BP_c (e.g. BP_c differences between regions in coarse sand sediments rather mirror the variability in biomass, than in abundance). A further reason for decreasing BP_c towards the south may rely on the expectation that conditions of higher food supply from the water column favour the presence of species which score lower in both motility and sediment reworking, causing a general reduction in BP_c . For example, Anthozoa as well as some other taxa that depend on food supply from the water column (e.g. *Ensis*), rather than on

sedimentary food, are indicated as key species in BENS (see Table 2). To examine a relationship between BP_c and primary production (used as proxy for food supply) we have compared our resulting BP_c maps with primary production layers (averaged from February to October) published by Melin (2013). In contrast to findings of Meyer et al. (2019), we found significant negative correlation between BP_c and primary production for the DENS region ($R=-0.53$, $p<0.001$), though it was positive for BENS and DEBS ($R=0.52$ and $R=0.70$, respectively, $p<0.001$), and not significant for ENCH.

4.3. Potential environmental drivers of biogeographic patterns of BP_c

It is important to account for differences in sediment habitat when assessing biogeographic patterns, as for example much of the functioning is undertaken by physical processes rather than biological processes in sand habitats, whilst the reverse is true in muddy sediments (Sciberras et al. 2017; Hale et al. 2017; Godbold et al. 2017). Accounting for spatial differences even at smaller scale of distinct seafloor morphologies was found crucial for improving management of goods and services delivered by marine ecosystems (Zeppilli et al., 2016).

Similar to previous findings, highest BP_c values were associated with fine sand sediments in DENS and BENS (Meyer et al. 2019; Braeckman et al. 2014; Breine et al. 2018), whereas it was lowest in medium to coarse permeable sands in DENS and in very shallow muddy sediments in BENS. This observed weak negative trend of BP_c with increasing median grain size in the German and Belgian parts of the North Sea could indicate that less species are adapted to the pressure of high exposure conditions (e.g. due to survival of only small and mobile species in highly dynamic areas).

Due to difference in conditions and settings across different benthic habitats of the four regions their formal comparison is challenging. For example, the environmental settings (e.g. with respect to organic matter loading, salinity) of muddy sediments in DEBS and those in the BENS are different and are expected to constrain slightly different communities. Key fine sand species in ENCH are partly corresponding to species in medium sands in BENS. The structural differences (composition, density, biomass and diversity) in communities are reflected in different magnitudes of estimated bioturbation potential and the relative importance of environmental drivers of BP_c for each area (Table 4).

Food availability was an important driver of the biogeographic patterns in BP_c in this study (see Table 4 and the discussion above). In the North Sea in general, biomass increases consistently in finer sediments and sediments with higher chlorophyll a content (Heip et al., 1992), but this is different in the Baltic Sea (Darr et al., 2014). In the DEBS in particular, also oxygen conditions and salinity were major drivers of the distribution of BP_c . Here hypoxia limits the distribution of species in the deeper bays with finer sediments,

and a strong salinity gradient drives the overall biodiversity (Darr et al., 2014; Zettler et al., 2017). Hypoxia affects the activities of benthic animals leading to decreased bio-irrigation and bioturbation rates, which are eventually eliminated when benthic animals have disappeared as a result of oxygen stress (Middelburg and Levin, 2009), with major consequences for sediment biogeochemistry and species interactions (Belley et al. 2010; Van Colen et al. 2012; Giffiths et al. 2017; Calder-Potts et al. 2018).

Unlike causal predictors like temperature, salinity, or primary production, water depth may be considered an indirect proxy integrating several (potentially not included) predictor variables (Reiss et al., 2015), such as human pressures. The depth ranges considered were relatively comparable across the four regional datasets, with the exception of BENS region, where also very shallow locations were included in the dataset. This is probably the reason why it was among the most important predictors for the BENS region, although in other regions depth displayed less influence on the variability of BP_c .

In the ENCH, current energy and temperature were among the most important predictors. Though we had no layer of fishing pressure available for this region, it is possible that the effect of high fishing pressure here is attenuated by the effects of hydrodynamics, with flatfish fisheries mostly associated with fine and medium sands (Hinz et al., 2006) and scallop fisheries - with coarse sand (Szostek et al., 2016). Particularly, strong fishing activity in this area can reduce or exclude the largest, generally fragile, species.

4.4. Temporal variability and implications of changes

The focus of our study is on the spatial patterns across regions, whereby temporal differences were beyond the scope of our analysis. This was justified by the fact that spatial variability of BP_c in our data exceeded the temporal variation (see Supplementary material S1, as well as Gogina et al. 2017 for justification in DEBS). Also, long-term studies in DENS reported stable spatial distribution of four major communities (e.g. Kröncke et al., 2011), although some structural changes were observed within each of them. According to Boyé et al. (2019), benthic spatial beta diversity structure remained remarkably stable and temporal variability was of small extent to the south-west of ENCH (based on the 2008-2014 data from monitoring of benthic macrofauna across the Brittany).

On the other hand, further studies suggest that temporal variation on the long and short terms require more attention. Meyer et al. (2019) detected a steady increase in BP_c across the south-eastern North Sea since 1986, with the exception of the central and northern Oysterground, where a significant drop in BP_c was found. They also revealed a shift in dominance of functional groups within major communities up to 2010–2015 that was related to anthropogenic pressures (fishery, seabed degradation), increasing sea surface temperature, food limitation, and de-eutrophication.

It is important to acknowledge that the replacement of one functional group by another could, but not necessarily, result in BP_c changes (see also Thomsen et al., 2017 for insights on post-extinction compensatory responses). The introduction of *Ensis leei*, a relatively large, abundant and very active species, is a good example of a shift that could completely modify the BP_c in the newly colonized areas. Moreover, considering the importance in the total BP_c in the DENS and BENS and the massive mortalities this species can exhibit (e.g. Dannheim and Rumohr, 2012), high temporal variations in the BP_c values following such events are not unlikely. This, and our results on the relationship between BP_c and species diversity, are also largely consistent with the meta-analysis findings of Gamfeldt et al. (2015) that showed tendency of more diverse communities to enhance levels of ecosystem function relative to the average monocultures, but to have no or negative effect on functioning relative to the ‘highest-performing’ (i.e. key) species.

4.5. Comparison and application of two modelling approaches

Overall patterns resulting from two modelling approaches were similar (and generally close to patterns resulting from interpolation), justifying the usefulness of both approaches, depending on the application of the model results. The direct modelling of BP_c was always closer to observations and interpolation approach (based on Kendall's τ estimates). Models derived by the “direct- BP_c ” approach (i) can be recommended to produce maps identifying potential bioturbation hot spots, irrespective of species contributing to them. The “species-resolved” approach (ii) can provide a better solution when impact of specific taxa is questioned. It allows differentiating between species responsible for the occurrence of those hot spots in different areas of the region, reflecting the suitability of conditions for particular bioturbation agents, and testing the scenarios of change in their distribution. The natural neighbour interpolation approach (iii) in turn provides the results most seconded by the observed values (i.e. generates most evidence-based distribution maps comparing with both modelling approaches that rely on the assumptions of parameterised links of BP_c to abiotic predictors). The obvious disadvantage of spatial interpolation, however, is the inability to predict and the lack of resolution in space between samples where observations are absent.

Our simplified application example helped to illustrate a potential application of the proposed models to quantify consequences of biodiversity changes for ecosystem functioning. This aspect was not the main focus of this study. Nevertheless, it raised some interesting points to consider in the discussion of this work. The resulting estimates showed that denitrification estimates mainly follow the distribution patterns in macrofauna, both in terms of diversity and BP_c . When comparing with models excluding 14

species, the highest relative reductions in denitrification emerged in the areas with lowest initial denitrification rates (Fig. 5E). Those results, placed aside with BENS maps of BP_c derived by two modelling approaches (Fig. 3, BENS A and B) suggest that those areas have remarkably low values of summed BP_c determined by key functional species at the regional scale, though values determined by direct BP_c approach are comparable with other areas of low- BP_c in this region. This suggests different levels of biodiversity and evenness in these areas of the BENS, which are in turn related to different degrees of change in denitrification rates after biodiversity loss. On the other hand, this can also simply be a result of model artefact, and the issue requires further investigation that is beyond the scope of this paper. We can only note that the functionally most important species at the regional scale also dominate in biomass and abundance (see Supplementary material S1.3), but possibly in these particular areas (with lowest estimated initial denitrification rates) other species, that are generally rare on regional scale, could determine the maintenance of ecosystem properties. Wohlgemuth et al. (2016) found that the most dominant species exert a disproportionate influence on functioning at low levels of evenness. However, a system with many species of low dominance and high evenness, where species-specific contributions are low, can be more resistant to change when comparing to situations with only few dominant species. Due to higher functional redundancy associated with high evenness, i.e. low contribution scenario, the disappearance of a species will not strongly destabilize the functioning. We would like to note that the presented example was most simple and easy to implement. Alternatively, the denitrification estimate could be based on BP_c based on original macrofauna data, interpolating values spatially using natural neighbour method, and subsequently repeating the exercise after removal of the species from the original dataset. Finally, it is important to highlight that this theoretical example works for regions where a close relationship is demonstrated between BP_c and ecosystem functions, as demonstrated in Braeckman et al. (2014). However, this is not the case everywhere and potential limitations of the method are discussed below.

4.6. Performance, flaws and limitations of BP_c modelling

There are several limitations associated with the models and BP_c index itself, which are related to regional low sampling efforts, validation of the index by measurements and limited knowledge on species traits.

Low model performance of many species-specific models was indicated for ENCH. This can be partly explained by the low number of stations in the dataset. In random forests, negative variance explained is a clear warning that the model might be overfitting a lot of noise in the data, and the ensemble of trees

fits little of the true patterns. However, similar general trends were found in the densely sampled BENS as well, suggesting that observed patterns for ENCH are realistic.

There is a clear level of uncertainty, which differed between models for the different key species in the “species-resolved” modelling approach (Supplementary material S4) and is further hindered after summation of the species-specific BP_p results to calculate the BP_c estimates. Presumably, model accuracy decreases with increasing number of key species, but precision increases. As such, the model result for BENS, where highest number of key species was considered, has the lowest accuracy. This consideration appeals for additional caution with regards to the results of our application example (Section 3.5).

Addressing the issue of the relation between BP_c and benthic processes, there is still a need for more experiments simultaneously investigating benthic mineralisation processes and macrofaunal functional traits to permit a more formal validation. Databases that collect experimental data worldwide now start to emerge, and they could greatly help to validate the index in the future. One good example is the recent publication by Solan et al. (2019) covering bioturbation intensity, ventilation rate, and mixing depth measurements of marine sediments (though high temporal variability and low spatial coverage of measurements included hinder large-scale spatial assessments).

Our level of knowledge on traits is good for a limited number of species and traits, but more discursive for the others, leading to the accumulation of minor mistakes or imprecisions. We argue that due to large number of included species, straightforward selection of relatively well-known traits and modalities, and multiple quality checks of trait scores by regional experts (Supplementary material S2), our modelling approaches to produce full-coverage maps, estimating BP_c values at a regional scale, are justified. Increased knowledge on species ecology and trait scores will indeed lead to changes in the absolute values of the modelled BP_c scores, but we are confident that the geographical patterns and relation with environmental variables are accurately reflected by our methodology.

We aimed to infer general patterns, compare and explore the differences in distribution, key contributing species and possible drivers of BP_c between the four regions. Common problems for such inter-regional comparisons are: 1 – inclusion of datasets unbalanced in size, covered period, species diversity and distribution of sediment types, that require a trade-off between data availability and consistency of analysis; 2 – due to high variability of species distribution occurring under similar conditions and limited sets of available predictors, low model accuracy for some species cannot be avoided.

4.7. A word of caution: utility of BP_c to reflect ecosystem functioning

Several studies have validated the performance of BP_c and similar indicators against measured bioturbation (e.g. Gogina et al., 2017; Queirós et al., 2015) and bioirrigation rates (e.g. Wrede et al., 2018), indicating that they are robust enough to be complementary, but are not an alternative to direct measurements (see e.g. Wohlgemuth et al., 2017). Importantly, such indicators are rather a proxy for functionally important ecosystem processes, and a combination of experimental and modelling work remains the most promising method to quantify the importance of ecosystem engineers on the biogeochemical functioning of aquatic ecosystems (Mermillod-Blondin, 2011). Furthermore, there is a need for more comprehensive descriptors to account for behavioural aspects affecting ecosystem functioning (Hale et al., 2014).

The general purpose of this paper was to give an indication of the relative role of bioturbation in generic terms. In this context, it is important to point out that BP_c was developed to reflect particle reworking (Solan et al., 2004), and not for the purpose of linking it with ecosystem functioning *per se*. The metric can be useful in this way, but care needs to be taken for its appropriate use and resulting conclusions, as its utility depends on whether or not it fits the functional data (e.g. Kristensen et al., 2012; Queirós et al., 2015; Gogina et al., 2018). For instance, BP_c does not always fit the data on nutrient fluxes: in cases it does, one important explanation can again be that the index reflects a process (such as particle displacement) that substantially contributes to the transport process. In other areas where it does not, the contribution of fauna is not important, e.g. when mineralization processes in permeable sediments are constrained by advective currents (Mermillod-Blondin, 2011). Subsequent papers have added bioirrigation to the metric (Wrede et al., 2018; Renz et al., 2018), which may probably be more appropriate when considering many of the functions we care about, such as nutrient cycling. Spatially explicit full-coverage layers of distribution of bioirrigation-based indices can be then obtained in a similar manner as was done here for BP_c . BP_c , as used in this paper, is more appropriate for mixing depths (Queirós et al., 2015) and sediment stability (Cozzoli et al., 2018).

Hence, and taking into account the regional variation reported here, BP_c should not be applied widely across different systems and in relation with many functions, before more work is done to understand when and where the metric is appropriate, and what the mechanistic basis behind it is.

In a perfect world, there would be no need for the BP_c metric, as we would have a value for per capita contributions for each species across a range of functions we are most interested in. However, we know very little about the functional role of individual species in terms of actual measurements. Our analysis of BP_c highlighted focus species requiring special attention in the regions considered. Yet BP_c is reflecting

only a summation of capacity based on coarse assumptions about species traits, biomass and density, whereas the actual contribution of individual species and organisms to processes in the real natural realm can by far not be resolved.

Conclusions

The executed multi-regional analysis allowed to identify regional differences in performance of macrofauna reflected by BP_c , which suggests that conservation and management strategies need to be region specific at scales less than, for example, the North Sea. Unlike most studies, we have highlighted species that appear to be important in terms of their functional contributions rather than biomass (or abundance) dominance. For many of these identified key species there are only few studies published yet.

Full-coverage maps of BP_c for each region were obtained, providing semi-quantitative information on functional aspects of macrofaunal communities and their major drivers. Both modelling algorithms provided satisfactorily results and predicted similar patterns of spatial distribution of BP_c ; the usefulness of both approaches for different scientific questions and management applications was demonstrated. Analysis of available data suggested large variation of bioturbation potential, and occurrence of high bioturbation capacity even under low diversity. Our results further highlight the difference in importance of environmental drivers in the different regions (see Table 4), suggesting that same predictors cannot be used in different biogeographic areas. A number of shortcomings buried in the index formulation and modelling approaches invoke caution in use of acquired information. Coarse modelling exercises like this can be useful for providing a large-scale picture that level out multiple sources of fine-scale spatial and temporal variability to managers and decision makers. However, it is impossible to overemphasize the necessity of experimental measurements for validation purposed and provisioning us with mechanistic details to develop the whole ecosystem-level understanding, including biogeochemical cycles, and disentangle multiple main linkages, overseen so far, in order to improve predictability and achieve sustainable governance (Hofmann et al., 2016).

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Supplementary material

Supplementary material S1: Map with sampling stations and sediment type layer, temporal and spatial variability of BP_c, lists of top 10 key taxa contributing to total BP_c and to total AFDW

Supplementary material S2: Species lists with traits scores per region

Supplementary material S3: List of available abiotic predictors, predictor's importance, partial correlation

Supplementary material S4: Model performance for BP_c and key species

Supplementary material S5: PERMANOVA, boxplots for AFDW, abundance and species richness, Functional Redundancy

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