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Disentangling the effect of space, time, and environmental and anthropogenic drivers on coastal macrobenthic β diversity in contrasting habitats over 15 years

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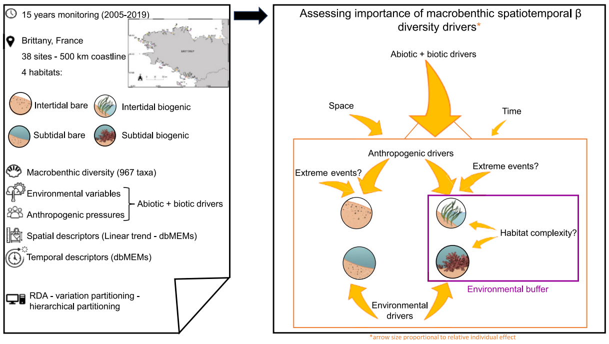
HIGHLIGHTS

- β diversity was mainly explained by environmental and anthropogenic variables
- Contribution of explanatory variables to β diversity was highly habitat-dependent
- Biogenic habitats mitigate the effect of environmental and anthropogenic pressures
- Anthropogenic variables were the most structuring in intertidal habitats
- Residual spatial and temporal variations were relatively weak in all habitats

GRAPHICAL ABSTRACT



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ABSTRACT

Coastal zones are biodiversity hotspots and deliver essential ecosystem functions and services, yet they are exposed to multiple and interacting anthropogenic and environmental constraints. The individual and cumulative effects of these constraints on benthic communities, a key component of coastal ecosystems, and their variability across space and time, remains to be thoroughly quantified to guide conservation actions. Here, we explored how the presence of biogenic habitats influences the response of benthic communities to natural and anthropogenic constraints. We investigated this effect in both intertidal and subtidal habitats exposed to different pressures. We used data collected in the North-East Atlantic over 15 years (2005–2019) as part of the REBENT monitoring program, covering 38 sites of bare sediments, intertidal seagrass beds and maerl beds. We collected a range of environmental variables and proxies of anthropogenic pressures and used variation and hierarchical partitioning with redundancy analyses to estimate their relative effect on macrobenthic communities. We used descriptors modeling spatial and temporal structures (dbMEMs) to explore the scale of their effects and potential

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missing predictors. The selected variables explained between 53 % and 64 % of macrobenthic β diversity depending on habitat and depth. Fishing pressures, sedimentary and hydrodynamics variables stood out as the most important predictors across all habitats while proxies of anthropogenic pressures were overall more important in intertidal habitats. In the intertidal, presence of biogenic habitat strongly modulated the amount of explained variance and the identity of the selected variable. Across both tidal levels, analysis of models' residuals further indicated that biogenic habitats might mitigate the effect of extreme environmental events. Our study provides a hierarchy of the most important drivers of benthic communities across different habitats and tidal levels, emphasizing the prominence of anthropogenic pressures on intertidal communities and the role of biogenic habitats in mitigating environmental changes.

1. Introduction

Coastal zones accommodate a large proportion of human population (Burke et al., 2001) and the ecosystems they support provide a variety of resources and valuable services (Costanza et al., 1997). However, they harbor some of the most threatened natural systems (Lotze et al., 2006; Halpern et al., 2008) since intensified human activities lead to degradation of key coastal habitats, their biodiversity, functions and ecosystem services they provide (Barbier et al., 2011; Bernhardt and Leslie, 2013). In addition to local human impacts, anthropogenically induced climate change is an increasing threat to coastal marine ecosystems, where it is occurring at a faster rate than on land (Burrows et al., 2011). Human activities can change the extent, frequency and magnitude of natural disturbances (He and Silliman, 2019) and these multiple stressors can interact (Thrush et al., 2021b), often in complex synergistic ways in marine systems (Crain et al., 2008). Therefore, the interactions between local, regional and global human impacts need to be considered to set up effective coastal management strategies (He and Silliman, 2019). In this context, long-term studies allow for detecting and quantifying ecological responses to drivers of ecosystem change and thereby enhancing our understanding of ecosystem processes (Lindenmayer et al., 2012), as already reported from various monitoring programs in coastal waters over the past decades (Cloern et al., 2016).

Benthic macrofauna is often used in monitoring programs of coastal marine ecosystems as indicator of changes, since most macrobenthic species have limited mobility (thus are exposed to the local physical environment), show various life spans and exhibit different tolerances to environmental stresses (Dauer, 1993). Moreover, they play important roles in marine ecosystems such as nutrient cycling, bioturbation and secondary production (Snelgrove, 1998). Many studies focusing on marine benthic ecology aimed to identify the different drivers responsible for spatial patterns structuring the communities and disentangle human impacts from natural gradients (e.g., Dutertre et al., 2013; Silberberger et al., 2019). However, we still have a limited understanding of the relationships between temporal and spatial variation in abiotic variables and the biological patterns in macrobenthic assemblages, and how they change over time (Ysebaert and Herman, 2002; McArthur et al., 2010). One central topic in community ecology is the estimation of the relative importance of the different processes controlling the changes in species composition and abundances in space and time (Anderson and Cribble, 1998). Using canonical analyses, the total variation of a species abundance matrix can be explained by partitioning it between different fractions (e.g., environmental variation, environmental variation without the spatial component, temporal variation etc.) (Borcard et al., 1992; Anderson and Cribble, 1998). Each of these fractions can be linked to different ecological processes (i.e., species sorting, mass-effect, neutral model or patch dynamics) (Leibold et al., 2004; Cottenie, 2005; Soininen, 2014; Legendre and Gauthier, 2014). The environmental fraction has often been shown to be the most structuring fraction of community variation compared to other fractions (e.g., spatial), especially in marine ecosystems (Cottenie, 2005; Soininen, 2014).

The environmental drivers mostly structuring the distribution of macrobenthic organisms are productivity, temperature and sediment composition (McArthur et al., 2010). Many studies have shown that sedimentary variables often explained most of the community variation at local and regional scales (e.g., Chauvel et al., 2024) although other variables clearly structure macrobenthic communities depending on the habitat considered, such as bathymetry, hydrodynamic conditions or physico-chemical properties of the water column (Ysebaert and Herman, 2002; Dutertre et al., 2013, 2015; Veiga et al., 2017; Couce et al., 2020). These environmental variables vary spatially and temporally and their relationship with biological patterns and processes in macrobenthic communities still needs to be assessed (Ysebaert and Herman, 2002; McArthur et al., 2010). In addition to these parameters, the type of habitat has also a significant influence on the variation of macrobenthic assemblages, as it is a major factor determining the occurrence of benthic species (Cottenie, 2005; Couce et al., 2020). For example, the presence of a foundation species can modify the extent of species niches through facilitation (Bulleri et al., 2016).

Anthropogenic pressures can also play a major role in macrobenthic β diversity (defined as the variation in community structure and composition among a set of sample units within a given spatial or temporal extent; Anderson et al., 2011, Legendre and De Cáceres, 2013) as they can strongly modify community structure and composition through direct or indirect effects (Thrush et al., 2021a). For example, fishing pressures can induce changes in community composition through the direct removal of species or by affecting food webs and sediment characteristics (Hily et al., 2008; Sciberras et al., 2018). Increasing human density and activity can induce an increase in waste and sewage, while land development for industrial and agricultural activities can lead to pollution, habitat destruction or degradation, and eutrophication (He and Silliman, 2019). Causes of coastal eutrophication are often bound within coastal ecosystems and their watersheds (Duarte et al., 2009) and can for example result in the development of green tides affecting benthic communities (Cloern, 2001; Quillien et al., 2018). Thus, human population density and activity have been widely used as a reasonable proxy of the relative magnitude of local human impacts (He and Silliman, 2019).

Brittany (France) is a biogeographic transition zone between the Northern European seas and the Lusitanian province (Spalding et al., 2007), which is characterized by a high diversity of benthic habitats and which is a hotspot of macrobenthic richness (Gallon et al., 2017), although subject to different aspects of global change and anthropogenic threats (e.g., Quillien et al., 2015, 2018; Ragueneau et al., 2018). It harbors widely distributed bare sedimentary habitats and more spatially limited biogenic habitats created by foundation species, but nonetheless important for the taxonomic and functional diversities of macrobenthic assemblages (Boyé et al., 2019). Maerl and seagrass beds are the two main biogenic habitats that can be found along the coasts of Brittany in soft substrates. They are both fragile and complex biotopes providing resources and shelters for a large variety of biota while being threatened by human activities (Airoldi and Beck, 2007). These habitats may mitigate the strength of abiotic factors' effects on macrobenthic communities by dampening environmental variation through the reduction of physical stress for example (Bulleri et al., 2018).

In this study, we used 15 years of benthic macrofauna monitoring, in 38 sites distributed along 500 km of Brittany coasts and located in four different soft-bottom habitats exposed to different abiotic constraints: two biogenic habitats associated with foundation species (i.e., seagrass and maerl beds) in the intertidal and the subtidal zones respectively, and two bare sedimentary habitats also in these two different tidal zones. To our knowledge, this is the first study of such spatial and temporal coverage using variation and hierarchical partitioning of macrobenthic communities between space, time, environmental and anthropogenic fractions. The main objectives were to (i) identify and compare spatial

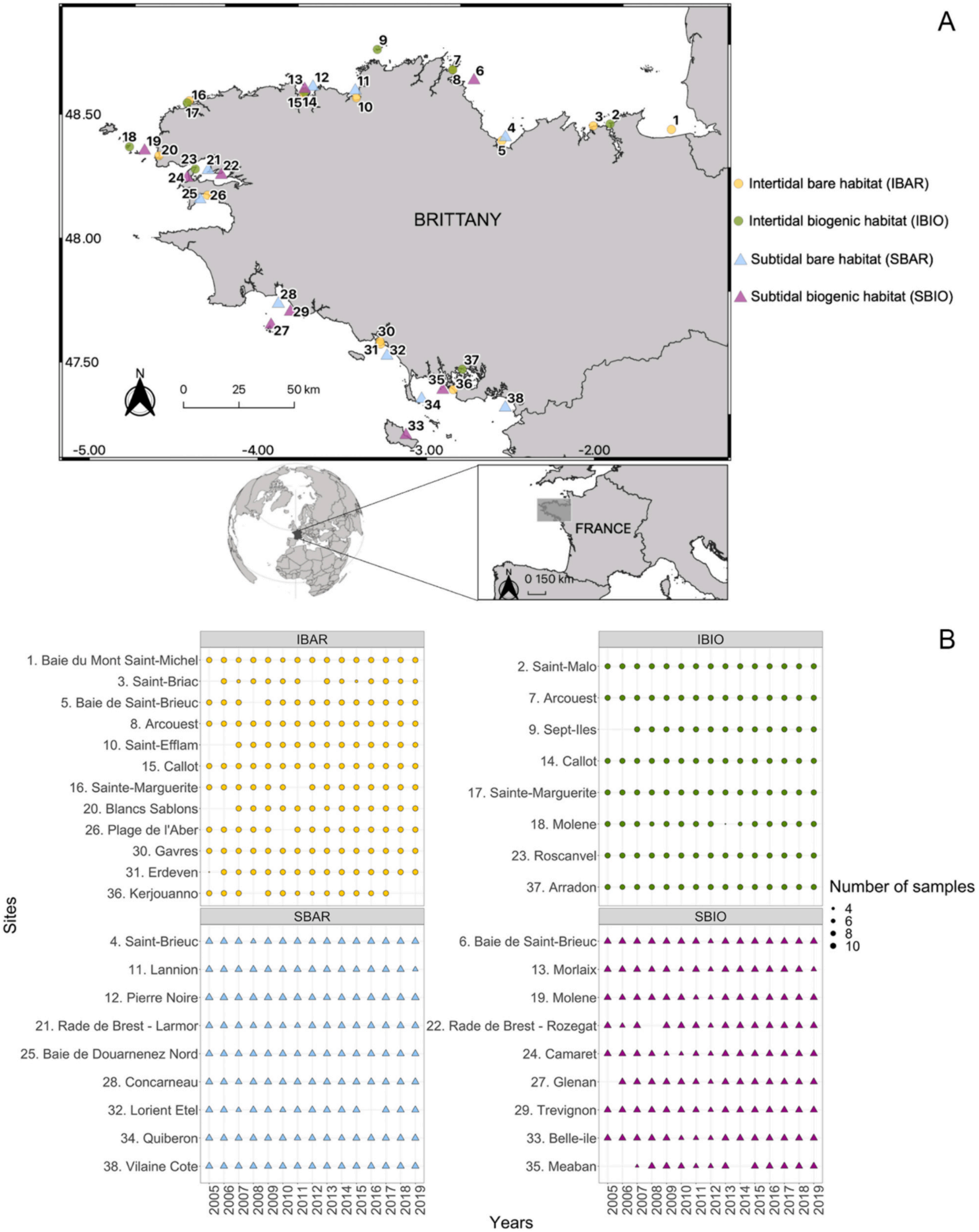


Fig. 1. A) Map of the sites in the four monitored habitats along the coasts of Brittany (France). (Sources: OpenStreetMap, European Environment Agency). B) Number of samples (cores in the intertidal and grabs in the subtidal) that were aggregated to estimate taxon abundances for each site in each habitat from 2005 to 2019.

and temporal patterns of benthic communities' structure and composition between four different habitats and (ii) identify and disentangle the importance of the different environmental and anthropogenic variables that drive the spatiotemporal dynamics of the benthic communities of the different habitats. We expect (i) differential community responses to the same abiotic conditions in biogenic versus bare soft bottom habitats, irrespective of the tidal zone. Indeed, biogenic habitats might mitigate the effects of environmental pressures on communities compared to bare ones (e.g., Bulleri et al., 2018; Jurgens et al., 2022). We also expect (ii) differential community responses between intertidal and subtidal habitats, as intertidal communities are exposed to both terrestrial and marine constraints (Helmuth et al., 2006), and communities' responses to environmental constraints might therefore occur more rapidly than in subtidal environments (Hinz et al., 2011).

2. Material and methods

2.1. Macrofauna sampling

Benthic communities have been monitored yearly since 2003 along the coasts of Brittany (France) within the REBENT program (http://www.rebent.org). We focused on four sedimentary habitats: intertidal sandy beaches, intertidal seagrass beds (formed by *Zostera marina*), subtidal soft sediments and subtidal maerl (or rhodolith) beds (principally formed by *Lithothamnion corallioides* and *Phymatolithon calcareum*). These four habitats are respectively referred to as intertidal bare habitat (IBAR), intertidal biogenic habitat (IBIO), subtidal bare habitat (SBAR) and subtidal biogenic habitat (SBIO) from this point forward.

At each site, three faunal samples were taken at each of three fixed sampling points distributed 200 m apart (using a 0.03 m^2 core in the intertidal and a 0.1 m^2 Smith-McIntyre grab in the subtidal; see Boyé et al., 2019), except for the Pierre Noire site (number 12 in Fig. 1), where 10 grab samples were taken at one point of the site. Sampling was performed between the end of February and the beginning of May, before the recruitment of most species in the region (Dauvin et al., 2007; Boyé et al., 2019). In the laboratory, specimens were sorted, counted and identified to the lowest possible taxonomic level (usually species). Since the acquisition and identification of specimens were not systematically carried out by the same people over the years, each recorded taxon was scrutinized by experts in benthic taxonomy and their names were checked thanks to the World Register of Marine Species (WoRMS Editorial Board, 2021) to ensure for taxonomic resolution consistency and minimize variation artefacts in the data.

To minimize the impact of missing data on the analyses, we selected sites that both had at least 3 core or grab samples in any particular year and <4 sampled years missing (out of 15). Samples were pooled to estimate abundances at the site level. This led to a selection of 38 sites monitored from 2005 to 2019 while keeping a spatial resolution covering the coasts of Brittany and encompassing most of the environmental settings found in this region (Boyé et al., 2017, 2019). Of these 38 sites, 12 were in IBAR, 8 in IBIO, 9 in SBAR and 9 in SBIO (Fig. 1). In total, over the 15 years and 4 habitats, the dataset included 550 observations and 967 taxa (Appendix A).

All data from the REBENT monitoring program (https://rebent.ifremer.fr) are available in the Quadrige database (https://envlit.ifremer.fr/Quadrige-la-base-de-donnees) and in the database of the marine observatory of the IUEM (available upon request: https://www-iuem.univ-brest.fr/observatoire).

2.2. Explanatory variables

2.2.1. Spatial and temporal patterns

To model spatial patterns, we used distance-based Moran's Eigenvector Maps (dbMEMs) which are linearly independent spatial descriptors that allow for modeling spatial structures over a wide range of spatial scales (Borcard and Legendre, 2002; Dray et al., 2006). For dbMEMs computation, distances among sites were calculated as the shortest paths along the coast following the methodology described in Appendix B. We also modeled a spatial linear trend using, at each site, the shortest distance along the coast from the northernmost site, consecutively to the southernmost site. Similarly, temporal patterns were modeled using dbMEMs on the temporal coordinates of the sampling dates among the 15 years monitored (Legendre and Gauthier, 2014). Because the temporal linear trend was not significant, we did not include it in the final models. In both cases, we only selected the dbMEMs accounting for positive spatial or temporal correlation (Borcard et al., 2018).

2.2.2. Abiotic and biotic explanatory variables

Abiotic and biotic explanatory variables included environmental variables, abiotic and biotic descriptors of the habitats, and proxies of anthropogenic pressures. These variables were extracted in situ at the time of the REBENT macrofauna sampling, or numerically computed a posteriori (see Appendix B). All data were estimated at the site level, some varying in time (spatiotemporal variation) and others not (spatial variation only) (Table 1).

Natural environmental variables included sediment characteristics (e.g., grain-size distribution), morphometric data of *Zostera marina* beds (i.e., *Zostera marina* morphological and structural traits), seawater properties and hydrodynamics variables (hydrology and hydrodynamics), climate data on land (meteorology), a proxy of wave exposure (fetch) and bathymetry (depth) (Table 1).

Proxies of anthropogenic pressures included the number of inhabitants (hab) in the vicinity of sites, the land surfaces covered by artificial (artif) or agricultural (agri) areas in the vicinity of sites or in watersheds in the vicinity of sites (see Appendix B for details), and fishing pressures according to the type of fishing carried out in each of the four habitats (Table 1 and Appendix B). The number of inhabitants stood as a proxy for human frequentation of the sites and activities in their vicinity as well as urbanization of the coastline, while land use and watersheds stood as a proxy for potential runoffs from industrial and agricultural areas, but also human activity in the vicinity of sites and potential eutrophication processes.

The in situ data had an annual temporal resolution since they were collected every year at the occasion of the macrofauna sampling. Spatiotemporal data from numerical models (i.e., "Hydrology & Hydrodynamics" and "Meteorology" data sets, Table 1) had a daily resolution. In order for these data to have the same temporal resolution as the macrofauna and in situ natural environmental data (i.e., one value per year), while taking into account their variability in the months preceding the sampling dates, we calculated the mean, standard deviation, minimum and maximum values of each variable, at each site, from the 1st of November of the previous year to the date of sampling. We made this choice in order to account for winter storms (typical of North-West France between November and March) (Leckebusch et al., 2006; Poppeschi et al., 2021) that could have an influence on the sampled communities (e.g., Harris et al., 2011; Corte et al., 2017). We did not consider the summer and autumn conditions in the year prior to sampling as they were considered too distant in time to be relevant predictors of the observed communities (Lessin et al., 2019).

All variables were quantitative and continuous, except for the semi-quantitative fishing pressure coded 'No', 'Low, 'High' according to the type of fishing practiced in each habitat.

The details of the protocols, numerical model products and techniques used to extract and calculate each of the variables can be found in Appendix B.

2.2.3. Natural environmental variables selection

Given the high number of explanatory variables, variable selection was performed for natural environmental variables (green color in Table 1). Within each dataset (corresponding to the column "Data" of Table 1), collinear variables were first removed using Variance Inflation

Factors (VIF) (Legendre and Legendre, 2012) with a threshold of 10 (Appendix C). Then, variable selection was performed for each habitat separately. Redundancy analyses (RDA) (Rao, 1964; Legendre and Legendre, 2012) were performed, with the response matrix being the community matrix of Hellinger-transformed taxa abundances in a given habitat, and the explanatory matrix including all natural environmental

Table 1

List of the abiotic and biotic explanatory datasets and their variables before selection, their abbreviations, how they were acquired, for which habitat, and examples of studies where these variables have been shown as potential drivers of macrofaunal β diversity. *For each variable of the “Hydrology & Hydrodynamics” and “Meteorology” datasets, the mean, standard deviation, minimum and maximum values from November 1st of the previous year to the date of sampling were taken. Number of inhabitants and land use surfaces were estimated at the buffer and/or watershed scale (see Appendix B). IBAR = intertidal bare habitat, IBIO =intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat. References cited in the table: Rees et al., 1977; Currie and Parry, 1996; Thrush et al., 1998; Snelgrove, 1998; Boström and Bonsdorff, 2000; Lerberg et al., 2000; Ellingsen, 2002; Gray, 2002; Ysebaert and Herman, 2002; Hovel et al., 2002; Lercari and Defeo, 2003; Dauvin et al., 2004; Blanchet et al., 2005; Lercari and Defeo, 2006; Lotze et al., 2006; Boström et al., 2006; Cardoso et al., 2008; Hily et al., 2008; Bouma et al., 2009; Grilo et al., 2011; Dutertre et al., 2013; Cloern et al., 2016; Veiga et al., 2017; Sciberras et al., 2018; Couce et al., 2020; Chauvel et al., 2024; Millot et al., 2024.

Acquisition	Data	Variables	Abbreviation	Habitat	Potential drivers of macrofauna diversity
Spatiotemporal data					
In situ	Sediments (grain-size distribution and organic matter content)	mean (μm) median (μm) trask or sorting index kurtosis (μm) gravels (%) sand (%) mud (%) organic matter (%)	mean.grain D50 So kurtosis gravel sand mud OM	🟡 🟢 △ ▲	Ellingsen 2002; Ysebaert and Herman 2002; Dauvin et al. 2004; Blanchet et al. 2005; Dutertre et al. 2013; Veiga et al. 2017; Chauvel et al. 2024
	Zostera marina morphological and structural traits	density (shoot.m^{-2}) leaf biomass (g.m^{-2}) root biomass (g.m^{-2}) mean sheath height (mm) mean leaf length (mm) leaf width (mm) number of leaves per shoot percentage of broken leaves (%)	density leaf.biom root.biom sheath.height leaf.length leaf.width leaves/shoot broken	🟢	Boström and Bonsdorff 2000; Hovel et al. 2002; Bouma et al. 2009; Millot et al. 2024
Numeric	Hydrology & Hydrodynamics*	bottom temperature (°C) salinity (psu) current velocity (m.s^{-1})	bottomT sal current	🟡 🟢 △ ▲	Snelgrove 1998; Gray 2002; Lercari and Defeo 2003, 2006; Dutertre et al. 2013; Couce et al. 2020
	Meteorology*	air temperature (°C) wind velocity (m.s^{-1}) total rainfall (mm) minimum air temperature (°C) maximum air temperature (°C) daily range temperature (°C)	T wind rain minT maxT drangeT	🟡 🟢	Rees et al. 1977; Boström and Bonsdorff 2000; Cardoso et al. 2008; Grilo et al. 2011
Spatial data					
Numeric	Fetch	fetch (km)	fetch	🟡 🟢 △ ▲	Rees et al. 1977; Hovel et al. 2002; Boström et al. 2006
	Depth	depth (m)	depth	△ ▲	Snelgrove 1998; Ellingsen 2002; Dauvin et al. 2004; Dutertre et al. 2013
	Population	number of inhabitants (log)	hab	🟡 🟢 △ ▲	Lerberg et al. 2000; Lotze et al. 2006
	Land use	artificial surface (km^2) agricultural area (km^2)	artif agri	🟡 🟢 △ ▲	Lerberg et al. 2000; Cloern et al. 2016
Expert	Fishing	recreational fishing professional fishing dredging	RF (No/Low/High) PF (No/Low/High) DR (No/Low/High)	🟡 🟢 🟡 △ ▲	Currie and Parry 1996; Thrush et al. 1998; Hily et al. 2008; Sciberras et al. 2018

🟡 IBAR 🟢 IBIO △ SBAR ▲ SBIO

🟩 Natural environment 🟧 Proxies of anthropogenic pressures variables remaining after VIF analysis for a given group of predictors. The Hellinger distance coefficient is equivalent to the Euclidean distance computed on the square root of species relative abundances. It does not give an excessive weight to rare or highly abundant species and has the advantage of fulfilling the metric and Euclidean properties (Legendre and Gallagher, 2001; Legendre and De Cáceres, 2013). Models were tested for significance using 999 permutations of the community data. As they were all significant, we proceeded with a forward selection of the environmental variables based on adjusted R^2 (Blanchet et al., 2008). No variable selection was done for anthropogenic proxies that were all retained for subsequent analyses and only positive spatial and temporal dbMEMs accounting for positive spatial or temporal correlation were kept (see Section 2.2.1) (Table 2).

2.3. Data analyses

β diversity was computed as the total variance of the Hellinger-transformed community matrix (Legendre and De Cáceres, 2013) in each habitat. First, to explain β diversity, a RDA was conducted in each habitat separately, between the community matrix of Hellinger-transformed taxa abundances (response matrix) and the matrices of selected abiotic and biotic explanatory variables (i.e., selected natural environmental variables + proxies of anthropogenic pressures; Table 2). In hierarchical partitioning, the individual contribution of a predictor is defined as its unique contribution to the total model plus its average shared contributions with the other predictors (Lai et al., 2022). As we were not able to assess the individual contribution of each selected abiotic and biotic explanatory variable by hierarchical partitioning as calculation speed is currently a limitation with the R package "rdacca.hp" (Lai et al., 2022), we estimated the importance of each selected abiotic and biotic explanatory variables in each habitat by conjointly looking at the proportion of variation explained (adjusted R^2) by each variable in simple (without other variables as condition) and partial (with other variables as condition) RDAs. We also plotted the average of residuals for each habitat and year combination to try to identify years and/or habitats where models based on selected abiotic and biotic explanatory variables either failed to explain the observed β diversity or, on the contrary, performed rather well. RDA models were tested for significance using 999 permutations of the community data.

Second, we conducted variation partitioning and hierarchical partitioning based on RDA analyses (Lai et al., 2022) with all variables of Table 2, to calculate the unique, shared and individual contributions of each matrix of predictors (i.e., natural environment matrix, proxy of anthropogenic pressures matrix, spatial linear trend, spatial dbMEMs matrix, temporal dbMEMs matrix) to the explained variation of communities within each habitat. We were able to compute the individual contribution in this case as the number of individual contributions was reduced to the number of matrices (i.e., 5). RDA models were tested for significance using 999 permutations of the community data. Individual contribution of each fraction in hierarchical partitioning was tested using 999 permutations with the "permu.hp" function of the R package "rdacca.hp" (Lai et al., 2022).

Note that analyses were carried out for each habitat separately and that Hellinger-transformed abundances, based on relative abundances, were used to minimize the effect of sample differences between habitats and tidal zones in the comparisons.

All analyses were conducted with the R programming language version 4.1.2 (R Core Team, 2021) and packages, "adespatial" (Dray et al., 2022), "vegan" (Oksanen et al., 2022) and "rdacca.hp" (Lai et al., 2022). Outputs from the "rdacca.hp" package were plotted using the "UpSetVP" package (Liu, 2022).

3. Results

Simple RDAs between the community matrix and the matrix of selected abiotic and biotic explanatory variables (i.e., selected natural environmental variables + proxies of anthropogenic pressures) were significant for all habitats ($p < 0.001$) and explained 49.4 % of total variation (adjusted R^2) in the intertidal bare habitat (IBAR), 61.6 % in the intertidal biogenic habitat (IBIO), 56.0 % in the subtidal bare habitat (SBAR) and 53.8 % in the subtidal biogenic habitat (SBIO) respectively. Based on model predictions, abiotic and biotic explanatory variables mostly distinguished communities of different sites within each habitat and generally better explained the spatial heterogeneity than the temporal one, especially for IBAR, IBIO and SBAR (Fig. 2). The main spatial patterns highlighted by the RDA and the identity of the predicted underlying drivers differed across habitats, although some commonalities appeared such as the important predicted role of sediment properties and of the degree of exposure of the sites, as well as the non-negligible role of anthropogenic pressures (Fig. 2). For instance, the number of inhabitants (hab) seemed to be an important predictor in each habitat.

The main community gradient predicted in IBIO distinguished sheltered muddy sites (on the left of the RDA, associated with annelids such as *Lumbrineris* spp. and *Golfingia (Golfingia) elongata* characteristic of fine muddy sands) from sites exposed to high wind and current velocities, associated with polychaetes such as *Spio* spp. or the amphipod *Urothoe poseidonis* which are characteristic of highly hydrodynamic environments (on the right). Proxies of anthropogenic pressures (in particular the type of land use (artif) and the number of inhabitants (hab)) drove the variation along the second axis of the RDA for that habitat. Although the predicted spatial patterns were markedly different in IBAR, an important role of site exposure and sediment properties was also visible: the two axes distinguishing the muddiest site at the bottom (Baie du Mont Saint-Michel (1)), from sites with highly variable sediment sizes on the top right, associated with *Acrocnida* spp. and *Donax vittatus* often found on exposed beaches, and sites with coarse sediments on the top left (Arcouest (8), Callot (15), Sainte-Marguerite (16) and Gavres (30)) associated with species such as *Apseudopsis latreillii* or *Notomastus latericeus* which proliferate in more enclosed environments (Fig. 2). Interestingly, most of the sites on the top left of the RDA are located close to IBIO sites (Fig. 1). However, a higher role of anthropogenic proxies, in particular fishery-related variables, was reported as a major discriminant of IBAR communities along the first RDA axis. In SBIO, sedimentary conditions discriminated one site, Trevignon (29), which also present a singular community dominated by *Pisidia longicornis* (Toumi et al., 2023), whereas depth and proxies of anthropogenic pressures (i.e., number of inhabitants (hab), land use (agri and artif)) explained the community difference between the three sites of Baie de Saint-Brieuc (6), Rade de Brest – Rozegat (22) and Camaret (24), and the other beds of Molene (19) or Belle-ile (33). Overall, RDA failed to explain spatial differences among the remaining SBIO sites (high convex hull overlaps), but rather explained temporal community differences within these sites (e.g., temporal dynamics within Morlaix (13) and Meaban (35) predicted from changes in current velocities and sediment properties). On the contrary, sites in SBAR were more dispersed and bathymetry (depth), percentage of mud (mud), current velocity (sd. current, min.current), fetch as well as fishing pressure (low professional fishing (PF.low)) played an important role in their dispersion along the two axes. The first axis of the RDA distinguished muddy sites with species characteristic of these environments such as *Maldane glebifex* and *Amphiura filiformis* (on the bottom right) from sites with fine sands and little organic matter associated with species characteristic of these environments such as *Fabulina fabula* (on the bottom left).While spatial heterogeneity was better reflected than in SBIO, it appeared from these first two RDA axes that temporal variation remained an important component of the explained variance in SBAR, contrary to the two intertidal habitats.

To assess the importance of each abiotic and biotic explanatory variable in explaining the variation of the communities in each habitat, we looked at the adjusted R^2 of each predictor in simple and partial RDAs (Fig. 3). In simple RDAs, the predictors with the highest importance in the four habitats were all related to fishing pressure (i.e., recreational fishing (RF) in IBAR and IBIO, professional fishing (PF) in SBAR and dredging (DR) in SBIO) while variables related to hydrodynamics (i.e., fetch and standard deviation of current velocity (s.d.current)) and sediment properties (i.e., sorting index (So) and percentage of mud (mud)) often ranked second or third (Fig. 3). The highest percentage of variation explained by a single variable was >15 % in IBAR, IBIO and SBIO but lower than 10 % in SBAR. Moreover, the explained variation was relatively equivalent between the different predictors in SBAR and IBIO, whereas predictors' importance was highly uneven in IBAR and SBIO.

In partial RDAs, explained variation of each predictor decreased in comparison to the simple RDAs, except for artificial surfaces (artif) and agricultural areas (agri) in IBAR. The predictor with the highest importance in simple RDAs remained the same in all habitats (i.e., recreational fishing (RF) in IBAR, professional fishing (PF) in SBAR and dredging (DR) in SBIO), except for IBIO where the number of inhabitants (hab) became the most important predictor after partialling out the variation explained by all other predictors (while it was recreational fishing (RF) in simple RDA). In SBAR, proxies of anthropogenic pressures showed increased effect compared to the other abiotic variables. This increased estimated effect of proxies of anthropogenic pressures in partial RDAs compared to simple RDAs, indicated that they explained a unique and different share of variation compared to the other variables, a feature that is consistent across habitats. Interestingly, some predictors became significant in partial RDA while they were not in simple RDA (e.g., mean of maximum air temperatures (mean.maxT) in IBAR and maximum bottom temperature (max.bottomT) in SBIO).

Mean of the residuals per year and habitat of the simple RDAs with all selected natural environmental variables and proxies of anthropogenic pressures are represented in Fig. 4. The higher the mean of the residuals, the more the models failed to explain the observed community variation in composition and structure. Residual means are represented for each habitat separately as total variation explained by the RDA models are different for each habitat, preventing comparison of residual values between habitats (unlike the adjusted R^2 which allows comparison as conducted above). However, variability in mean residual values can be compared between habitats, and IBAR (Fig. 4A) showed the highest temporal variability in the residual values. In this habitat, the model seemed to be less effective at explaining β diversity during the first 4 years of monitoring (2005–2008) compared to the rest of the time series. Interestingly, in IBIO (Fig. 4B), the highest mean residual values were also found during these first 4 years of the monitoring but with less marked differences with the rest of the time series compared to IBAR. In the subtidal zone, the efficiency of the model to explain β diversity appeared more stable over time in the biogenic habitat (Fig. 4D) compared to the bare one (Fig. 4C), although the range of residual values

Table 2
Selected natural environmental variables, proxies of anthropogenic pressures and dbMEMs kept in each habitat for the analyses. Z.m = *Zostera marina*, Sp. Linear = Spatial linear trend, Sp. = Spatial, Tp. = Temporal, dbMEMs = distance-based Moran's Eigenvector maps, s.d. = standard deviation, min = minimum, max = maximum, IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat. The number of eigenvectors (MEMs) kept in Sp. dbMEMs and Tp. dbMEMs corresponds to the number of eigenvectors accounting for positive spatial or temporal correlation. Variables abbreviations and descriptions are detailed in Table 1.

Habitat	Sediments	Hydrology & Hydrodynamics	Meteorology	*Z.m* traits	Anthropogenic	Sp. Linear	Sp. dbMEMs	Tp. dbMEMs
IBAR	OM kurtosis So mean.grain mud	fetch s.d. current min current s.d. sal max sal min bottomT mean bottomT	s.d. wind min wind s.d. maxT max maxT mean maxT max T		hab agri artif RF PF	spatial linear trend	MEMS 1 to 2	MEMs 1 to 6
IBIO	OM kurtosis So D50 mud	fetch s.d. current min current s.d. sal max sal min bottomT	s.d. wind max wind max maxT mean maxT mean minT	leaf.width density	hab agri artif RF	spatial linear trend	MEMS 1 to 2	MEMs 1 to 6
SBAR	OM kurtosis mud	depth fetch s.d. current min current s.d. sal max sal max bottomT min bottomT			hab agri artif PF	spatial linear trend	MEMS 1 to 2	MEMs 1 to 6
SBIO	OM kurtosis mean.grain D50 mud	depth fetch s.d. current min current s.d. sal max sal max bottomT min bottomT			hab agri artif DR	spatial linear trend	MEMS 1 to 2	MEMs 1 to 6

🟩 Natural environment 🟧 Proxies of anthropogenic pressures 🟦 Space 🟪 Time is still narrower in SBAR compared to IBAR.

When adding spatial and temporal predictors (i.e., spatial linear trend (Sp.linear), spatial dbMEMs (Sp.dbMEMs), and temporal dbMEMs (Tp.dbMEMs)) as explanatory variables in the models (on top of the variables describing natural environmental conditions and anthropogenic pressures), explanatory power increased from 49.4 % to 53.2 % in IBAR, 61.6 % to 64 % in IBIO, 56.0 % to 59.5 % in SBAR and 53.8 % to 56.4 % in SBIO (Fig. 5). In hierarchical partitioning, each group of explanatory variables had different and significant individual contributions (Appendix D) to the global models: anthropogenic

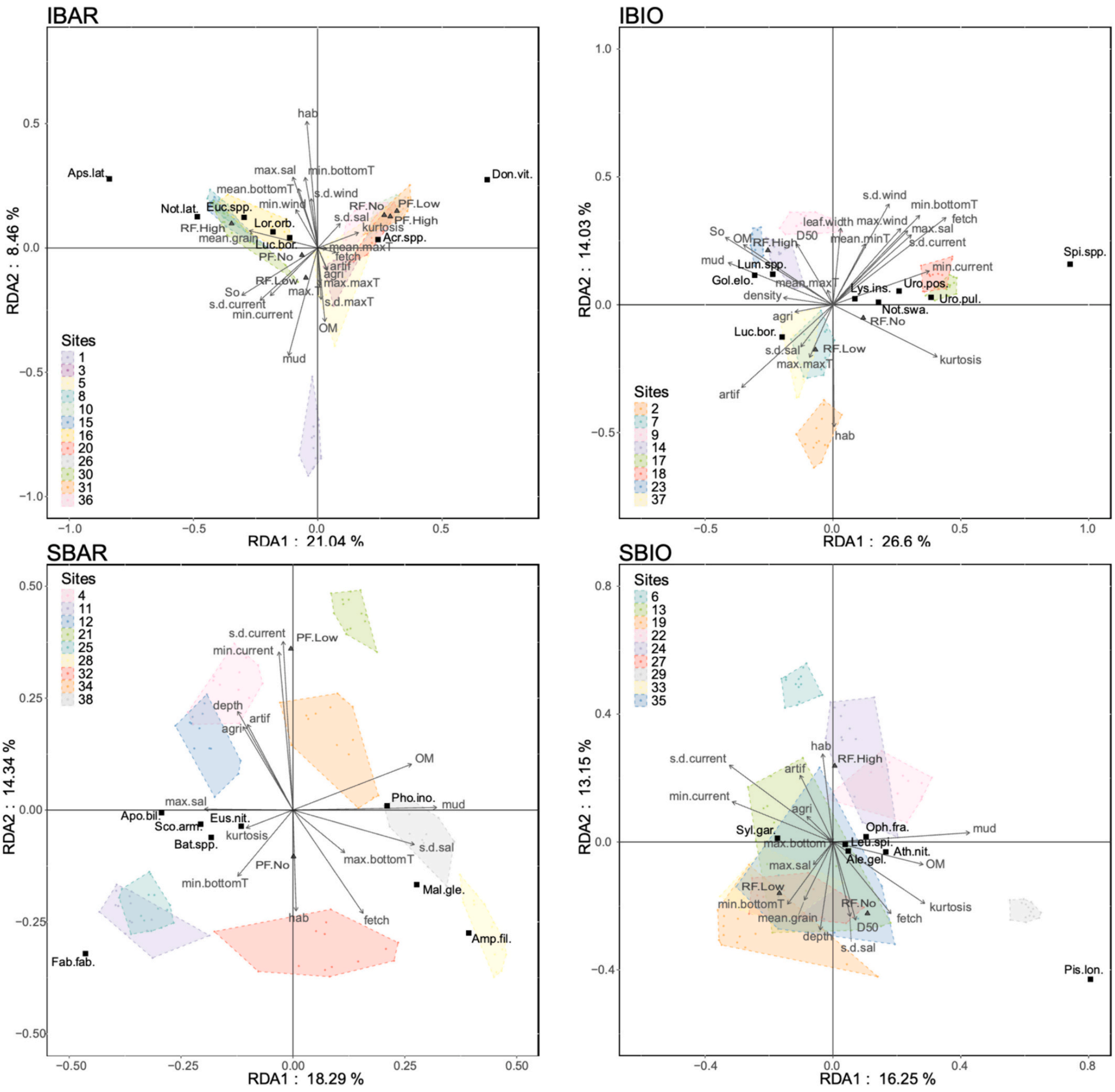


Fig. 2. RDA triplots (scaling 2 – weighted average) for each habitat (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat); only the first two canonical axes are represented. The percentages represent the proportion of total variation explained by each axis. Arrows represent the abiotic and biotic explanatory variables. Triangular points are the centroids of each level of the categorical variables (i.e., fishing pressure). Squares represent a subset of taxa whose variances along these two axes represent >30 % in IBAR, >40 % in IBIO, >40 % in SBAR and >30 % in SBIO of their total variances (assessed with the function "goodness" of the "vegan" package). Points represent the fitted observations (i.e., one site at one year); all observations from a single site are grouped within a convex hull. Species abbreviations: Aps.lat. = *Apseudopsis latreillii*, Not.lat. = *Notomastus latericeus*, Euc.spp. = *Euclymene* spp., Lor. orb. = *Loripes orbiculatus*, Luc.bor. = *Lucinoma borealis*, Acr.spp. = *Acrocnida* spp., Don.vit. = *Donax vittatus*, Lum.spp. = *Lumbrineris* spp., Gol.elo. = *Golfingia (Golfingia) elongata*, Lys.ins. = *Lysianassa insperata*, Not.swa. = *Nototropis swammerdamei*, Uro.pos. = *Urothoe poseidonis*, Uro.pul. = *Urothoe pulchella*, Spi.spp. = *Spio* spp., Fab.fab. = *Fabulina fabula*, Apo.bill. = *Aponuphis bilineata*, Sco.arm. = *Scoloplos armiger*, Bat.spp. = *Bathyporeia* spp., Eus.nit. = *Euspira nitida*, Mal.gle. = *Maldane glebifex*, Pho.ino. = *Pholoe inornata*, Amp.fil. = *Amphiura filiformis*, Syl.gar. = *Syllis garciai*, Leu.spi. = *Leucothoe spinicarpa*, Ale.gel. = *Alentia gelatinosa*, Oph.fra. = *Ophiothrix fragilis*, Ath.nit. = *Athanas nitescens*, Pis.lon = *Pisidia longicornis*. Full description of abiotic and biotic explanatory variables' abbreviations can be found in Table 1.

pressure proxy matrix (Prox.anthro) and natural environmental variables matrix (Environment) had higher individual contributions in each habitat, followed by the multi-scale spatial structures (spatial dbMEMs (Sp.dbMEMs)), the linear spatial trend (Sp.linear) and the temporal structure variables (temporal dbMEMs (Tp.dbMEMs)). The latter were significant in hierarchical partitioning but not in simple RDAs (Appendix E), contrary to the fraction explained by spatial dbMEMs, suggesting that temporal dynamics were of minor extent compared to the spatial variation of communities. Overall, most of the spatial and temporal structure in the variation and dynamics of the communities was well described by the natural environmental variables and anthropogenic predictors, as indicated by the very low individual contribution of spatial and temporal dbMEMs (< 2.5 % for both). Nonetheless, the partial RDAs indicated that there were still significant spatial and temporal structures unexplained by these variables (Appendix E). Notably, the fraction explained by temporal dbMEMs became significant in partial RDAs (Appendix E) and explained a higher proportion of variation than the unique fraction explained by the spatial predictors (Fig. 5), suggesting that the environmental and anthropogenic variables mostly captured spatial signals. This was illustrated by the amount of explained variation cumulatively represented by the fractions shared by the spatial predictors with either the natural environmental variables, the proxies of anthropogenic pressures, or both (Fig. 5). There were, however, important differences between bare and biogenic habitats in how these different shared fractions contributed to the total explained variation, meaning that the spatial signals captured by the anthropogenic and natural environmental variables differed between these two habitat types. Finally, a high proportion of community variation was explained by the shared fraction between the anthropogenic and environmental variables (i.e., abiotic and biotic explanatory variables) alone, representing the effects of these variables that are not spatially or temporally structured (at least with the spatial and temporal descriptors used). The latter is higher in biogenic habitats compared to bare ones. However, the fraction unique to anthropogenic variables and the one unique to natural environmental ones show the opposite pattern, being higher in bare habitats compared to biogenic ones. Hence, the overall amount of variation explained by anthropogenic and natural environmental variables that is not spatially or temporally structured seems fairly equivalent across habitats.

4. Discussion

4.1. Efficiency of abiotic and biotic variables in explaining spatial and temporal β diversity

Previous meta-analysis showed that the amount of community variation explained by environmental variables is on average higher in estuarine and marine ecosystems than in freshwater or terrestrial ones (Soininen, 2014). Yet, results are highly variable across studies so that the fraction explained by environmental variables in marine ecosystems can be lower than 20 % or higher than 70 %, with a median value around 40 % (Soininen, 2014). Here, RDA models with the selected abiotic and biotic explanatory variables explained from 49.4 % to 61.6 % of the β diversity in the four habitats. In the same study area, Dutertre et al. (2013) showed that environmental variables explained 51 % of the β diversity of subtidal soft sediments while Quillien et al. (2015) obtained models explaining from 15 % to 72 % of community variations in sandy beaches. Likewise, in intertidal seagrasses communities, environmental variables explained 9 % to 76 % of β diversity in northern New Zealand (using canonical correspondence analysis - CCA; Turner et al., 1999), and up to 25.6 % in the northern Baltic Sea (using RDA; Boström et al., 2006). In Northeast Brazil, CCA between environmental variables and benthic invertebrate community explained 30 % of the total variance (Costa et al., 2021). The heterogeneity of these results may bear some methodological imprints (e.g. use of CCA or RDA, use of different sets of environmental variables; Soininen, 2014) but may also be representative of meaningful ecological variation. For instance, Soininen (2014) found that traits of the species considered (e.g. dispersal mode, trophic position) could explain some heterogeneity observed across studies. Here, we show that the amount of explained community variation may also depend on the type of habitat (bare versus biogenic) and the tidal zone of the ecosystems.

Here, space and time had no important individual effect compared to the natural environmental variables and proxies of anthropogenic pressures, indicating that our abiotic and biotic variables certainly characterized the most important predictors of macrobenthic community variation. In our study, the spatial structure clearly dwarfed temporal variations. Time had the lowest individual importance, yet its individual contribution in hierarchical partitioning, as well as its unique fraction in variation partitioning, were still significant (Appendices D and E). This unique fraction can be interpreted as neutral drift in the communities, which means variation in species demography caused by random reproduction and survival of individuals due to species interactions (e.g, competition, predator-prey interactions, etc.) (Legendre and Gauthier, 2014). Regarding spatial descriptors, only two positive dbMEMs were generated to model positive spatial correlations. Therefore, the spatial dbMEMs only achieved to model large scaled spatial structures (Appendix F). Likewise, the spatial linear trend represented distance from the northern to the southern site along the coast, a broad-scale spatial structure often captured by one dbMEM especially in the biogenic habitats (Appendix F). Thus, fine scale structures (which represent spatial correlation produced by neutral biotic processes such as ecological drift or random dispersal), were missed and could not be modeled in the spatial fraction (Borcard et al., 2018). This means that, in variation partitioning, environmental variables and proxies of anthropogenic pressures captured broad-scale spatial patterns (i.e., the fractions shared with spatial descriptors). Yet, most of the explained variance was not shared with spatial or temporal descriptors. Hence, contrary to what has been shown in other regions (Menegotto et al., 2019; Carvalho et al., 2023) our results suggest a stronger influence of local variation rather than broad-scale regional processes.

4.2. Relative roles of natural and anthropogenic factors

Hierarchical partitioning showed that the natural environmental variables had a high individual importance in explaining community β diversity. In particular, hydrodynamics and grain-size distribution variables played an important role in communities' β diversity. Sediment characteristics are a determining factor that control the presence and abundance of soft-bottom fauna as each species can tolerate a specific sediment particle range (Snelgrove and Butman, 1994) and hydrodynamics can alter these sedimentary environments, thus these variables have often been demonstrated to be important drivers of macrofauna β diversity (Gray, 2002; Hily et al., 2008; Dutertre et al., 2013; Veiga et al., 2017; Couce et al., 2020; Chauvel et al., 2024).

Nearly all studies that explored the main sources of community variation in marine ecosystems before, including the meta-analyses from Cottenie (2005) and Soininen (2014), only took into account environmental variables and did not include proxies of anthropogenic pressures. Here, in terms of explanatory power, natural environmental variables were followed by or at least equivalent to the proxies of anthropogenic pressures. Adding the set of proxies of anthropogenic pressures to the models with only selected natural environmental variables increased the explanatory power of our models, especially in bare habitats (the percentage of explained variation rose from 33.1 % to 49.4 % in IBAR, 53.0 % to 61.6 % in IBIO, 43.5 % to 56.0 % in SBAR and 46.2 % to 53.8 % in SBIO; Appendix E). This highlights the importance of understanding and accounting for the spatial and temporal distribution of anthropogenic pressures (e.g., Burrows et al., 2014; Halpern et al., 2015) to explain and accurately predict the current distribution of benthic species and communities, especially for ecosystems under such high anthropogenic pressures (Korpinen et al., 2021).

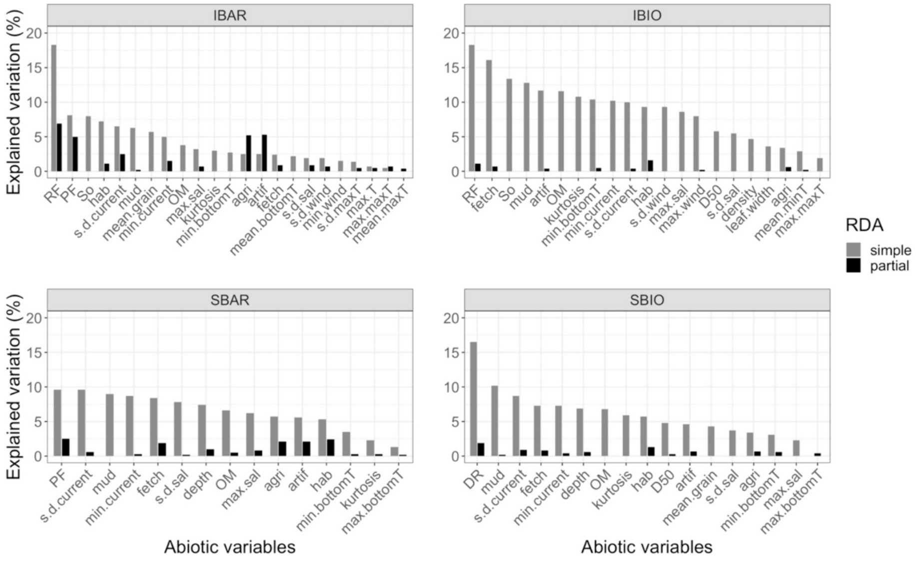


Fig. 3. Explained variation (adjusted R^2) of each selected natural environmental variables and proxies of anthropogenic pressures separately, either in simple RDA (without all other variables as conditions) or in partial RDA (with all other variables as conditions), within each habitat (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat). Only significant abiotic and biotic explanatory variables from simple or partial RDA models are presented ($p < 0.05$). Variable abbreviations are detailed in Table 1.

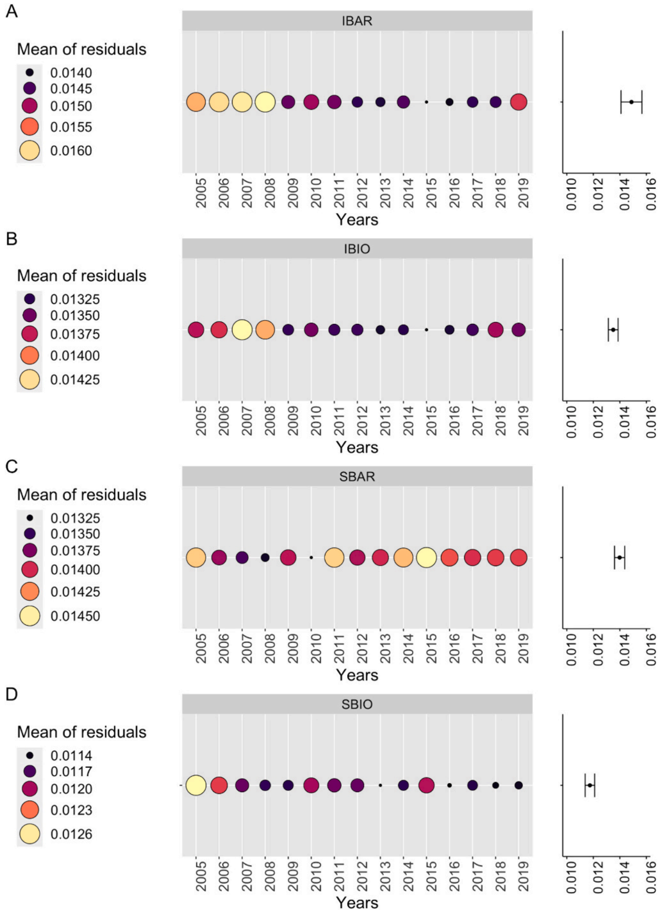
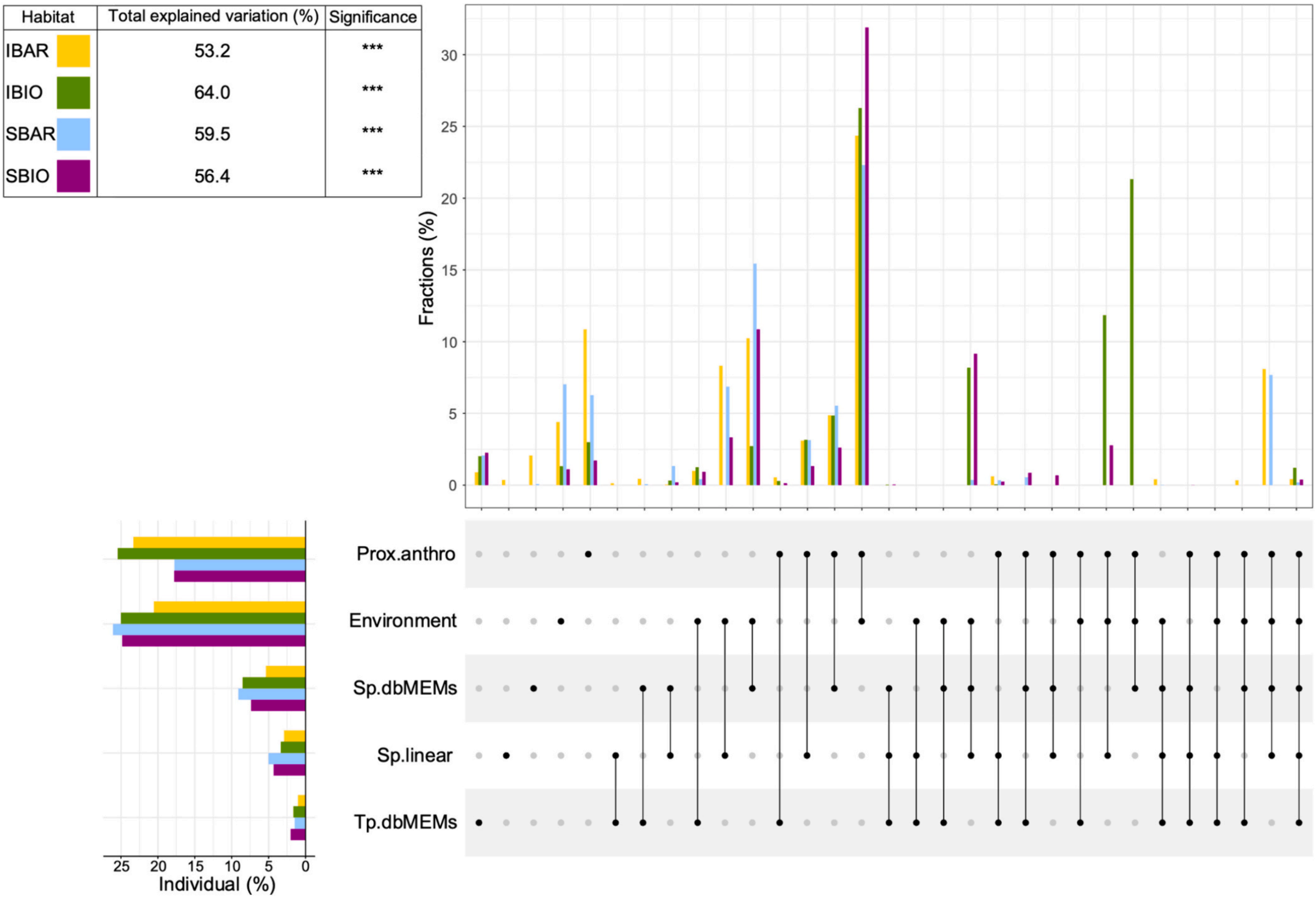


Fig. 4. RDA models' residual means for each year and habitat: A) intertidal bare habitat (IBAR), B) intertidal biogenic habitat (IBIO), C) subtidal bare habitat (SBAR), D) subtidal biogenic habitat (SBIO). Marginal plots represent marginal mean (point) +/− marginal standard deviation (whiskers).

The individual importance of proxies of anthropogenic pressures was higher in the intertidal zone. These pressures were surely better characterized for intertidal habitats since we used land data and we estimated the values for the subtidal sites from the values of the closest intertidal ones (see Appendix B). Moreover, it is also very likely that the effect of anthropogenic pressures would be more mitigated in the subtidal zone (Bacouillard et al., 2020). Among the proxies of anthropogenic pressures, fishing pressures explained a high proportion of variation in simple RDAs. However, part of that explained variation could also be explained by other variables in IBIO, SBAR and SBIO, as shown by the reduced amount of variation it explained in the partial RDAs. Thus, some factors may confound the perceived effect of fishing pressures: as fishing depends on the species present in the communities and because the sites were dominated by different taxa, the amount of variation explained by the fishing variables could be linked to the fact that they reflect the spatial variation of the different sites' communities. For instance, professional fishing is associated with sites dominated by *Donax* spp. in IBAR (Fig. 2). Alternatively, specific environmental conditions could be favorable or detrimental to fishing activities or the targeted taxa: for example, *Donax vittatus* is characteristic of wave exposed sandy bottoms (Allen and Moore, 1987). Moreover, there can be an interaction between natural and fishing disturbances as communities already exposed and adapted to high levels of natural disturbance may show fewer variations in their composition and structure due to fishing pressures (Hiddink et al., 2006). Yet, fishing can have a direct impact on the fauna (e.g., by increasing mortality of certain species, favoring other species by reducing predation etc.) and indirect ones by modifying habitat characteristics (e.g., sediment resuspension, habitat destruction etc.) (Hall-Spencer and Moore, 2000; Hily et al., 2008; Sciberras et al., 2018). These effects may overlap/correlate and/or combine with natural stressors (Bowler et al., 2020; Stockbridge et al., 2020), which could explain their shared fraction of explained variation.

Overall, the natural environmental variables and proxies of anthropogenic pressures seemed, in variation partitioning, to be highly correlated and they appeared to be spatially structured. This spatial structure can be explained by the fact that proxies of anthropogenic pressures do not present temporal variation (Table 1; Appendix B) and that, at the scale of the study area, the spatial variation of natural environmental variables can be more important than the temporal variations (Toumi et al., 2023). Moreover, as developed above for



Habitat	Total explained variation (%)	Significance
IBAR 🟨	53.2	***
IBIO 🟩	64.0	***
SBAR 🟦	59.5	***
SBIO 🟪	56.4	***

Fig. 5. Variation and hierarchical partitioning between the community matrix and each explanatory matrix within each habitat (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat). The top left table gives the total explained variation and significance of the global RDA models in each habitat (*** = $p < 0.001$). The barplot on the bottom left shows the individual contribution of each explanatory matrix assessed by hierarchical partitioning. The plot on top represents the percentage of variation (adjusted R^2) explained by the different matrices in variation partitioning (fractions <0 are not represented). The lower panel indicates the matrices taken into account as explanatory (black dots) or conditional (gray dots).

fishing pressure, this may indicate that human activities overlap/correlate in particular types of environments, or that environmental and anthropogenic pressures might have a combined effect on macrofauna communities. Interestingly however, in IBAR the high proportion of variance explained by recreational fishing (RF) or professional fishing (PF) explained some aspects of community variation that were not explained by other variables (high R^2 in partial RDAs). Other proxies of anthropogenic pressures (artificial surfaces (artif), agricultural areas (agri) and number and inhabitants (hab)) also stood out as important in partial RDAs, in the bare habitats especially. These proxies, that can characterize pollution, eutrophication or human use of the different sites, have therefore distinct signatures on the community variation across this region. For example, watersheds with urban and industrial development have already been demonstrated to alter hydrodynamics processes, to have an impact on the levels of chemical contaminants and to increase the severity and frequency of hypoxia episodes in tidal creeks where macrobenthic species were characterized by a low richness and abundances (Lerberg et al., 2000).

4.3. Role of biogenic habitats

Abiotic and biotic explanatory variables explained higher proportions of variance in the intertidal biogenic habitat (61.6 % in IBIO) than in the intertidal bare habitat (49.4 % in IBAR), while the difference was smaller between the bare (56 % in SBAR) and biogenic (53.8 % in SBIO) habitats in the subtidal zone.

In IBIO, we used biotic environmental explanatory variables that described the morphology of the foundation species, specifically shoot density (density) and leaf widths (leaf.width) of *Zostera marina*. These variables have been shown to influence the density and diversity of benthic macrofauna in seagrass meadows (Boström and Bonsdorff, 2000; Hovel et al., 2002; Bouma et al., 2009; Millot et al., 2024). This suggests that taking into account habitat complexity variables might improve the quality of the model and better describe macrobenthic community variation, except if these variables are collinear with abiotic ones. Indeed, collinearity between abiotic and biotic variables may explain the low explanatory power of seagrass descriptors (IBIO; Fig. 3). Along the coasts of Brittany, different water bodies follow one another and have different physico-chemical properties (Morice et al., 2020). This environmental gradient might influence the presence of different morphological types of the two biogenic habitats (Boyé et al., 2021; Jardim et al., 2022) and by cascading effects, the community that lives in. The shared fraction between abiotic and habitat complexity variables therefore represents both indirect effect of environmental conditions, mediated by changes in foundation species (Millot et al., 2024), and potential interaction between abiotic variables and foundation species (e.g, Watt and Scrosati, 2013). However, even if some indirect effects mediated by seagrass responses were highlighted by previous studies (Millot et al., 2024; Muller et al., 2023) in the region, the direct effects of environmental conditions seem to be the main drivers of community variation in intertidal seagrass beds. In the subtidal, habitat complexity of maerl beds monitored in Brittany is currently being investigated and quantified (Jardim et al., 2022). Rhodolith morphologies can affect macrofauna community structure as well (Berlandi et al., 2012; Solano-Barquero et al., 2022). A natural perspective of this study will be to quantify the shared and unique effects of maerl descriptors. Interestingly however, differences between biogenic and bare habitats in the subtidal were minor compared to those in the intertidal.

The different community response between intertidal habitats might be explained by the fact that biogenic habitats mitigate mostly the effect of extreme events but not of average spatial variation per se (Jurgens and Gaylord, 2018; Jurgens et al., 2022). The highly dynamic nature of intertidal habitats is only partially characterized by our natural environmental variables that summarize average variation of climatological conditions (but not extreme events or annual/seasonal variability, see Fig. 4 and the following paragraph). By mitigating extreme events (e.g., Peterson et al., 2004; Maxwell et al., 2017), IBIO may lead to more predictable communities given our dataset, while in IBAR, different timing of disturbances across sites may blur the relationship with our set of abiotic variables. Indeed, less disturbed communities are more likely to show signs of deterministic niche processes than communities frequently disturbed by extreme events, which are more prone to appear as stochastic or neutral (Bracewell et al., 2017).

Analyzing the residuals of RDA models with only abiotic and biotic explanatory variables allowed evaluating to what extent simple RDAs failed to explain the community variation, on average, for each year and habitat. In IBAR, the model was less successful in characterizing β diversity during the first four years of the monitoring (2005–2008), especially in 2008 that showed the highest values of residuals. Interestingly, in March 2008 a high-energy storm hit the French Atlantic coast and the western part of the English Channel, which resulted in morphological changes, and transport of intertidal bare sediment in the region (Fichaut and Suanez, 2011). Such extreme modifications of beach morphodynamics are known to have deep impacts on macrofaunal communities (Harris et al., 2011). This supports the hypothesis that our models did not adequately capture the effects of extreme events on the communities. Although we tried to take into account the variability of the temporally varying environmental variables by computing the minimum, maximum and standard deviation of their values during the months preceding the sampling dates, we may not have characterized well enough the extreme events of short duration that could have impacted the communities (e.g., Hobday et al., 2016). Moreover, drivers of macrobenthos dynamics acting at larger spatial scales such as the North Atlantic Oscillation (NAO) or the Atlantic Multidecadal Oscillation (AMO) were not taken into account in our models and might have improved our capacity to model the temporal variability of the communities (Drinkwater et al., 2003; Nye et al., 2014). Even though the residual values were slightly higher during the first four years of the time series in IBIO, they did not show as much variability as observed in IBAR. In the subtidal zone, the efficiency of the model to explain β diversity also appeared more stable over time in the biogenic habitat, although differences were less marked between the biogenic and bare habitat. Again, this supports the hypothesis that biogenic habitats may mitigate the effect of environmental variables, especially in extreme physical environments such as the intertidal zone (Crain and Bertness, 2006).

5. Conclusion

This study was based on a recent method coupling variation and hierarchical partitioning and using more than four explanatory fractions mixing natural environmental variables, proxies of anthropogenic pressures, space and time, rarely used all together to better understand benthic macrofauna dynamics. It took into account proxies of anthropogenic pressures acquired with an original method and which have demonstrated their efficiency in the analyses, suggesting the importance to characterize and integrate these variables in studies on the drivers of benthic macrofauna β diversity. Environmental variables and proxies of anthropogenic pressures mostly explained local variation of the communities (i.e. variance not shared with spatial or temporal dbMEMs) but also captured broad-scale spatial patterns (shared with spatial dbMEMs). The spatial structure clearly dwarfed temporal variations. The individual effect of proxies of anthropogenic pressure was at least equivalent to the environmental fraction in the intertidal, highlighting the need to incorporate descriptors of anthropogenic pressures more frequently in studies of this kind. Fishing pressure (Appendix B) had a very strong importance in the beaches, more than in the other three habitats. Overall, the amount of explained community variation varied depending on the type of habitat (bare versus biogenic) and the tidal zone of the ecosystems. Biogenic habitats seemed to mitigate the effect of the environment, more so in exposed areas such as the intertidal zone. This study shows that intertidal habitats, and in particular sandy beaches, are sensitive to anthropogenic pressures, however, the indicators of anthropogenic pressures used here varied only in space and not in time. More precise quantification of these pressures over time would provide a better understanding of their interactions with environmental pressures and their synchrony or asynchrony.

CRediT authorship contribution statement

Chirine Toumi: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Olivier Gauthier:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jacques Grall:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Éric Thiébaut:** Writing – review & editing, Investigation. **Aurélien Boyé:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.173919.

References

Airoldi, L., Beck, M., 2007. Loss, status and trends for coastal marine habitats of Europe. In: Gibson, R., Atkinson, R., Gordon, J. (Eds.), *Oceanography and Marine Biology*. CRC Press (Oceanography and Marine Biology - an Annual Review), Pp. 345–405. https://doi.org/10.1201/9781420050943.ch7. Available at.

Allen, P.L., Moore, J.J., 1987. Invertebrate macrofauna as potential indicators of sandy beach instability. Estuar. Coast. Shelf Sci. 24 (1), 109–125. Available at: https://doi.org/10.1016/0272-7714(87)90008-4.

Anderson, M.J., Cribble, N.A., 1998. Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. Aust. J. Ecol. 23 (2), 158–167. Available at: https://doi.org/10.1111/j.1442-9993.1998.tb00713.x.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14 (1), 19–28. Available at: https://doi.org/10.1111/j.1461-0248.2010.01552.x.

Bacouillard, L., Baux, N., Dauvin, J.-C., Desroy, N., Geiger, K.J., Gentil, F., Thiébaut, É., 2020. Long-term spatio-temporal changes of the muddy fine sand benthic community of the bay of seine (eastern English Channel). Mar. Environ. Res. 161, 105062. Available at: https://doi.org/10.1016/j.marenvres.2020.105062.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81 (2), 169–193. Available at: https://doi.org/10.1890/10-1510.1.

Berlandi, R.M., Figueiredo, M.A. de O., Paiva, P.C., 2012. Rhodolith morphology and the diversity of Polychaetes off the southeastern Brazilian coast. J. Coast. Res. 28 (1), 280–287. Available at: https://doi.org/10.2112/11T-00002.1.

Bernhardt, J.R., Leslie, H.M., 2013. Resilience to climate change in coastal marine ecosystems. Annu. Rev. Mar. Sci. 5 (1), 371–392. Available at: https://doi.org/10.1146/annurev-marine-121211-172411.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. Ecology 89 (9), 2623–2632. Available at: https://doi.org/10.1890/07-0986.1.

Blanchet, H., de Montaudouin, X., Chardy, P., Bachelet, G., 2005. Structuring factors and recent changes in subtidal macrozoobenthic communities of a coastal lagoon, Arcachon Bay (France). Estuar. Coast. Shelf Sci. 64 (4), 561–576. Available at: https://doi.org/10.1016/j.ecss.2005.03.016.

Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol. Model. 153 (1), 51–68. Available at: https://doi.org/10.1016/S0304-3800(01)00501-4.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73 (3), 1045–1055. Available at: https://doi.org/10.2307/1940179.

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical Ecology With R. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-71404-2 (Use R!). Available at:

Boström, C., Bonsdorff, E., 2000. Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Mar. Ecol. Prog. Ser. 205, 123–138. Available at: https://doi.org/10.3354/meps205123.

Boström, C., O'Brien, K., Roos, C., Ekebom, J., 2006. Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape. J. Exp. Mar. Biol. Ecol. 335 (1), 52–73. Available at: https://doi.org/10.1016/j.jembe.2006.02.015.

Bouma, T.J., Olenin, S., Reise, K., Ysebaert, T., 2009. Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgol. Mar. Res. 63 (1), 95–106. Available at: https://doi.org/10.1007/s10152-009-0146-y.

Bowler, D.E., Bjorkman, A.D., Dornelas, M., Myers-Smith, I.H., Navarro, L.M., Niamir, A., Supp, S.R., Waldock, C., Winter, M., Vellend, M., Blowes, S.A., Böhning-Gaese, K., Bruelheide, H., Elahi, R., Antão, L.H., Hines, J., Isbell, F., Jones, H.P., Magurran, A. E., Cabral, J.S., Bates, A.E., 2020. Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. People Nat. 2 (2), 380–394. Available at: https://doi.org/10.1002/pan3.10071.

Boyé, A., Legendre, P., Grall, J., Gauthier, O., 2017. Constancy despite variability: local and regional macrofaunal diversity in intertidal seagrass beds. J. Sea Res. 130, 107–122. Available at: https://doi.org/10.1016/j.seares.2017.06.004.

Boyé, A., Thiébaut, É., Grall, J., Legendre, P., Broudin, C., Houbin, C., Le Garrec, V., Maguer, M., Droual, G., Gauthier, O., 2019. Trait-based approach to monitoring marine benthic data along 500 km of coastline. Divers. Distrib. 25 (12), 1879–1896. Available at: https://doi.org/10.1111/ddi.12987.

Boyé, A., Gauthier, O., Becheler, R., Le Garrec, V., Hily, C., Maguer, M., Grall, J., 2021. Drivers and limits of phenotypic responses in vulnerable seagrass populations: *Zostera marina* in the intertidal. J. Ecol. https://doi.org/10.1111/1365-2745.13791, pp. 1365-2745.13791. Available at:

Bracewell, S.A., Johnston, E.L., Clark, G.F., 2017. Latitudinal variation in the competition-colonisation trade-off reveals rate-mediated mechanisms of coexistence. Ecol. Lett. 20 (8), 947–957. Available at: https://doi.org/10.1111/ele.12791.

Bulleri, F., Bruno, J.F., Silliman, B.R., Stachowicz, J.J., 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. Funct. Ecol. 30 (1), 70–78. Available at: https://doi.org/10.1111/1365-2435.12528.

Bulleri, F., Eriksson, B.K., Queirós, A., Airoldi, L., Arenas, F., Arvanitidis, C., Bouma, T.J., Crowe, T.P., Davoult, D., Guizien, K., Iveša, L., Jenkins, S.R., Michalet, R., Olabarria, C., Procaccini, G., Serrão, E.A., Wahl, M., Benedetti-Cecchi, L., 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. PLoS Biol. 16 (9), e2006852. Available at: https://doi.org/10.1371/journal.pbio.2006852.

Burke, L., Kura, Y., Kassem, K., Revenga, C., Spalding, M., McAllister, D., Caddy, J., 2001. Coastal Ecosystems. World Resources Institute Washington, DC.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K. M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., Schwing, F.B., Sydeman, W.J. and Richardson, A.J. (2011) 'The pace of shifting climate in marine and terrestrial ecosystems', Science, 334(6056), pp. 652–655. Available at: https://doi.org/https://doi.org/10.1126/science.1210288.

Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., Halpern, B.S., Hoegh-Guldberg, O., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Sydeman, W.J., Ferrier, S., Williams, K.J. and Poloczanska, E.S. (2014) 'Geographical limits to species-range shifts are suggested by climate velocity', Nature, 507(7493), pp. 492–495. Available at: doi:https://doi.org/10.1038/nature12976.

Cardoso, P.G., Raffaelli, D., Lillebø, A.I., Verdelhos, T., Pardal, M.A., 2008. The impact of extreme flooding events and anthropogenic stressors on the macrobenthic communities' dynamics. Estuar. Coast. Shelf Sci. 76 (3), 553–565. Available at: https://doi.org/10.1016/j.ecss.2007.07.026.

Carvalho, S., Alsaffar, Z., Ellis, J., Alghamdi, H., Cúrdia, J., 2023. Broad-scale spatial distribution patterns of soft-sediment macrobenthic communities in the Red Sea. Front. Mar. Sci. 10, 1072342. Available at: https://doi.org/10.3389/fmars.2023.1072342.

Chauvel, N., Raoux, A., Weill, P., Dezilleau, L., Méar, Y., Murat, A., Poizot, E., Foveau, A., Desroy, N., Thiébaut, É., Dauvin, J.-C., Pezy, J.-P., 2024. Sediment grain size and benthic community structure in the eastern English Channel: species-dependent responses and environmental influence. Mar. Pollut. Bull. 200, 116042. Available at: https://doi.org/10.1016/j.marpolbul.2024.116042.

Cloern, J., 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. 210, 223–253. Available at: https://doi.org/10.3354/meps210223.

Cloern, J.E., Abreu, P.C., Carstensen, J., Chauvaud, L., Elmgren, R., Grall, J., Greening, H., Johansson, J.O.R., Kahru, M., Sherwood, E.T., Xu, J., Yin, K., 2016. Human activities and climate variability drive fast-paced change across the world's estuarine–coastal ecosystems. Glob. Chang. Biol. 22 (2), 513–529. Available at: https://doi.org/10.1111/gcb.13059.

Corte, G.N., Schlacher, T.A., Checon, H.H., Barboza, C.A.M., Siegle, E., Coleman, R.A., Amaral, A.C.Z., 2017. Storm effects on intertidal invertebrates: increased beta diversity of few individuals and species. PeerJ 5, e3360. Available at: https://doi.org/10.7717/peerj.3360.

Costa, D. de A., de Lucena, R.F.P., da Silva, F. de A., da Silva, G.M.B., Massei, K., Christoffersen, M.L., Dolbeth, M., 2021. Importance of rhodoliths as habitats for benthic communities in impacted environments. Reg. Stud. Mar. Sci. 48, 102055. Available at: https://doi.org/10.1016/j.rsma.2021.102055.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387 (6630), 253–260. Available at: https://doi.org/10.1038/387253a0.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecol. Lett. 8 (11), 1175–1182. Available at: https://doi.org/10.1111/j.1461-0248.2005.00820.x.

Couce, E., Engelhard, G.H. and Schratzberger, M. (2020) 'Capturing threshold responses of marine benthos along gradients of natural and anthropogenic change', J. Appl. Ecol. Edited by R. Pinto, 57(6), pp. 1137–1148. Available at: doi:https://doi.org/10.1111/1365-2664.13604.

Crain, C.M. and Bertness, M.D. (2006) 'Ecosystem engineering across environmental gradients: implications for conservation and management', BioScience, 56(3), pp. 211–218. Available at: doi:https://doi.org/10.1641/0006-3568(2006)056[0211:EEAEGI]2.0.CO;2.

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11 (12), 1304–1315. Available at: https://doi.org/10.1111/j.1461-0248.2008.01253.x.

Currie, D., Parry, G., 1996. Effects of scallop dredging on a soft sediment community: a large-scale experimental study. Mar. Ecol. Prog. Ser. 134, 131–150. Available at: https://doi.org/10.3354/meps134131.

Dauer, D.M., 1993. Biological criteria, environmental health and estuarine macrobenthic community structure. Mar. Pollut. Bull. 26 (5), 249–257. Available at: https://doi.org/10.1016/0025-326X(93)90063-P.

Dauvin, J.-C., Thiébaut, E., Gesteira, J.L.G., Ghertsos, K., Gentil, F., Ropert, M., Sylvand, B., 2004. Spatial structure of a subtidal macrobenthic community in the bay of Veys (Western Bay of Seine, English Channel). J. Exp. Mar. Biol. Ecol. 307 (2), 217–235. Available at: https://doi.org/10.1016/j.jembe.2004.02.005.

Dauvin, J.-C., Ruellet, T., Desroy, N., Janson, A.-L., 2007. The ecological quality status of the bay of seine and the seine estuary: use of biotic indices. Mar. Pollut. Bull. 55 (1), 241–257. Available at: https://doi.org/10.1016/j.marpolbul.2006.04.010.

Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Model. 196 (3–4), 483–493. Available at: https://doi.org/10.1016/j.ecolmodel.2006.02.015.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N. and Wagner, H.H. (2022) 'adespatial: Multivariate Multiscale Spatial Analysis'. Available at: https://CRAN.R-project.org/package=adespatial (Accessed: 2 October 2022).

Drinkwater, K.F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C.H., Ottersen, G., Pershing, A.J., Walker, H., 2003. The response of marine ecosystems to climate variability associated with the North Atlantic oscillation. In: Hurrell, J.W., Kushnir, Y., Ottersen, G., Visbeck, M. (Eds.), Geophysical Monograph Series.

American Geophysical Union, Washington, D. C, pp. 211–234. Available at: https://doi.org/10.1029/134GM10.

Duarte, C.M., Conley, D.J., Carstensen, J. and Sánchez-Camacho, M. (2009) 'Return to neverland: shifting baselines affect eutrophication restoration targets', Estuar. Coasts, 32(1), pp. 29–36. Available at: doi:https://doi.org/10.1007/s12237-008-9111-2.

Dutertre, M., Hamon, D., Chevalier, C., Ehrhold, A., 2013. The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. ICES J. Mar. Sci. 70 (2), 294–308. Available at: https://doi.org/10.1093/icesjms/fss170.

Dutertre, M., Grall, J., Ehrhold, A., Hamon, D., 2015. Environmental factors affecting maerl bed structure in Brittany (France). Eur. J. Phycol. 50 (4), 371–383. Available at: https://doi.org/10.1080/09670262.2015.1063698.

Ellingsen, K., 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. Mar. Ecol. Prog. Ser. 232, 15–27. Available at: https://doi.org/10.3354/meps232015.

Fichaut, B., Suanez, S., 2011. Quarrying, transport and deposition of cliff-top storm deposits during extreme events: Banneg Island, Brittany. Mar. Geol. 283 (1), 36–55. Available at: https://doi.org/10.1016/j.margeo.2010.11.003.

Gallon, R.K., Lavesque, N., Grall, J., Labrune, C., Gremare, A., Bachelet, G., Blanchet, H., Bonifácio, P., Bouchet, V.M.P., Dauvin, J.-C., Desroy, N., Gentil, F., Guerin, L., Houbin, C., Jourde, J., Laurand, S., Le Duff, M., Le Garrec, V., de Montaudouin, X., Olivier, F., Orvain, F., Sauriau, P.-G., Thiebaut, É., Gauthier, O., 2017. Regional and latitudinal patterns of soft-bottom macrobenthic invertebrates along French coasts: results from the RESOMAR database. J. Sea Res. 130, 96–106. Available at: https://doi.org/10.1016/j.seares.2017.03.011.

Gray, J., 2002. Species richness of marine soft sediments. Mar. Ecol. Prog. Ser. 244, 285–297. Available at: https://doi.org/10.3354/meps244285.

Grilo, T.F., Cardoso, P.G., Dolbeth, M., Bordalo, M.D., Pardal, M.A., 2011. Effects of extreme climate events on the macrobenthic communities' structure and functioning of a temperate estuary. Mar. Pollut. Bull. 62 (2), 303–311. Available at: https://doi.org/10.1016/j.marpolbul.2010.10.010.

Hall-Spencer, J.M., Moore, P.G., 2000. Scallop dredging has profound, long-term impacts on maerl habitats. ICES J. Mar. Sci. 57 (5), 1407–1415. Available at: https://doi.org/10.1006/jmsc.2000.0918.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319 (5865), 948–952. Available at: https://doi.org/10.1126/science.1149345.

Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J. S., Rockwood, R.C., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nat. Commun. 6 (1), 7615. Available at: https://doi.org/10.1038/ncomms8615.

Harris, L., Nel, R., Smale, M., Schoeman, D., 2011. Swashed away? Storm impacts on sandy beach macrofaunal communities. Estuar. Coast. Shelf Sci. 94 (3), 210–221. Available at: https://doi.org/10.1016/j.ecss.2011.06.013.

He, Q., Silliman, B.R., 2019. Climate change, human impacts, and coastal ecosystems in the Anthropocene. Curr. Biol. 29 (19), R1021–R1035. Available at: https://doi.org/10.1016/j.cub.2019.08.042.

Helmuth, B., Mieszkowska, N., Moore, P., Hawkins, S.J., 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. Annu. Rev. Ecol. Evol. Syst. 37 (1), 373–404. Available at: https://doi.org/10.1146/annurev.ecolsys.37.091305.110149.

Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E., Piet, G.J., 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Can. J. Fish. Aquat. Sci. 63 (4), 721–736. Available at: https://doi.org/10.1139/f05-266.

Hily, C., Le Loc'h, F., Grall, J., Glémarec, M., 2008. Soft bottom macrobenthic communities of North Biscay revisited: long-term evolution under fisheries-climate forcing. Estuar. Coast. Shelf Sci. 78 (2), 413–425. Available at: https://doi.org/10.1016/j.ecss.2008.01.004.

Hinz, H., Capasso, E., Lilley, M., Frost, M., Jenkins, S., 2011. Temporal differences across a bio-geographical boundary reveal slow response of sub-littoral benthos to climate change. Mar. Ecol. Prog. Ser. 423, 69–82. Available at: https://doi.org/10.3354/meps08963.

Hobday, A.J., Alexander, L.V., Perkins, S.E., Smale, D.A., Straub, S.C., Oliver, E.C.J., Benthuysen, J.A., Burrows, M.T., Donat, M.G., Feng, M., Holbrook, N.J., Moore, P.J., Scannell, H.A., Sen Gupta, A., Wernberg, T., 2016. A hierarchical approach to defining marine heatwaves. Prog. Oceanogr. 141, 227–238. Available at: https://doi.org/10.1016/j.pocean.2015.12.014.

Hovel, K.A., Fonseca, M.S., Myer, D.L., Kenworthy, W.J., Whitfield, P.E., 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Mar. Ecol. Prog. Ser. 243, 11–24. Available at: https://doi.org/10.3354/meps243011.

Jardim, V.L., Gauthier, O., Toumi, C., Grall, J., 2022. Quantifying maerl (rhodolith) habitat complexity along an environmental gradient at regional scale in the Northeast Atlantic. Mar. Environ. Res. 181, 105768 https://doi.org/10.1016/j.marenvres.2022.105768.

Jurgens, L.J. and Gaylord, B. (2018) 'Physical effects of habitat-forming species override latitudinal trends in temperature', Ecol. Lett. Edited by G. Diaz-Pulido, 21(2), pp. 190–196. Available at: doi:https://doi.org/10.1111/ele.12881.

Jurgens, L.J., Ashlock, L.W., Gaylord, B., 2022. Facilitation alters climate change risk on rocky shores. Ecology 103 (2), e03596. Available at: https://doi.org/10.1002/ecy.3596.

Korpinen, S., Laamanen, L., Bergström, L., Nurmi, M., Andersen, J.H., Haapaniemi, J., Harvey, E.T., Murray, C.J., Peterlin, M., Kallenbach, E., Klančnik, K., Stein, U., Tunesi, L., Vaughan, D., Reker, J., 2021. Combined effects of human pressures on Europe's marine ecosystems. Ambio 50 (7), 1325–1336. Available at: https://doi.org/10.1007/s13280-020-01482-x.

Lai, J., Zou, Y., Zhang, J., Peres-Neto, P.R., 2022. Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the rdacca. hp R package. Methods Ecol. Evol. 13 (4), 782–788.

Leckebusch, G., Koffi, B., Ulbrich, U., Pinto, J., Spangehl, T., Zacharias, S., 2006. Analysis of frequency and intensity of European winter storm events from a multi-model perspective, at synoptic and regional scales. Clim. Res. 31, 59–74. Available at: https://doi.org/10.3354/cr031059.

Legendre, P. and De Cáceres, M. (2013) 'Beta diversity as the variance of community data: dissimilarity coefficients and partitioning', Ecol. Lett. Edited by H. Morlon, 16 (8), pp. 951–963. Available at: doi:https://doi.org/10.1111/ele.12141.

Legendre, P. and Gallagher, E.D. (2001) 'Ecologically meaningful transformations for ordination of species data', Oecologia, 129(2), pp. 271–280. Available at: doi: https://doi.org/10.1007/s004420100716.

Legendre, P., Gauthier, O., 2014. Statistical methods for temporal and space–time analysis of community composition data. Proc. R. Soc. B Biol. Sci. 281 (1778), 20132728. Available at: https://doi.org/10.1098/rspb.2013.2728.

Legendre, P. and Legendre, L.F.J. (2012) 'Numerical ecology 3rd edn, Vol. 24', Developments in Environmental Modelling. Oxford, UK: Elsevier [Preprint].

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7 (7), 601–613. Available at: https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Lerberg, S.B., Holland, A.F., Sanger, D.M., 2000. Responses of tidal creek macrobenthic communities to the effects of watershed development. Estuaries 23 (6), 838. Available at: https://doi.org/10.2307/1353001.

Lercari, D., Defeo, O., 2003. Variation of a sandy beach macrobenthic community along a human-induced environmental gradient. Estuar. Coast. Shelf Sci. 58, 17–24. Available at: https://doi.org/10.1016/S0272-7714(03)00043-X.

Lercari, D., Defeo, O., 2006. Large-scale diversity and abundance trends in sandy beach macrofauna along full gradients of salinity and morphodynamics. Estuar. Coast. Shelf Sci. 68 (1), 27–35. Available at: https://doi.org/10.1016/j.ecss.2005.12.017.

Lessin, G., Bruggeman, J., McNeill, C.L. and Widdicombe, S. (2019) 'Time scales of benthic macrofaunal response to pelagic production differ between major feeding groups', *Front. Mar. Sci.*, 6. Available at: https://doi.org/10.3389/fmars.2019.00015 (Accessed: 4 February 2023).

Lindenmayer, D.B., Likens, G.E., Andersen, A., Bowman, D., Bull, C.M., Burns, E., Dickman, C.R., Hoffmann, A.A., Keith, D.A., Liddell, M.J., Lowe, A.J., Metcalfe, D.J., Phinn, S.R., Russell-Smith, J., Thurgate, N., Wardle, G.M., 2012. Value of long-term ecological studies. Austral Ecol. 37 (7), 745–757. Available at: https://doi.org/10.1111/j.1442-9993.2011.02351.x.

Liu, Y., 2022. UpSetVP: An alternative visualization of VPA and HP in Canonical Analysis. Available at: https://CRAN.R-project.org/package=UpSetVP.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312 (5781), 1806–1809. Available at: https://doi.org/10.1126/science.1128035.

Maxwell, P.S., Eklöf, J.S., van Katwijk, M.M., O'Brien, K.R., de la Torre-Castro, M., Boström, C., Bouma, T.J., Krause-Jensen, D., Unsworth, R.K.F., van Tussenbroek, B. I., van der Heide, T., 2017. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems – a review. Biol. Rev. 92 (3), 1521–1538. Available at: https://doi.org/10.1111/brv.12294.

McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D., Radke, L.C., 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuar. Coast. Shelf Sci. 88 (1), 21–32. Available at: https://doi.org/10.1016/j.ecss.2010.03.003.

Menegotto, A., Dambros, C.S., Netto, S.A., 2019. The scale-dependent effect of environmental filters on species turnover and nestedness in an estuarine benthic community. Ecology 100 (7), e02721. Available at: https://doi.org/10.1002/ecy.2721.

Millot, J., Grall, J., Toumi, C., Maguer, M., Boyé, A., 2024. Quantifying the direct and indirect relationships linking the environment, seagrass, and their associated fauna. Ecosphere 15 (2), e4708. Available at: https://doi.org/10.1002/ecs2.4708.

Morice, G., Bizzozero, L. and Fortune, M. (2020) Atlas DCE Loire - Bretagne. Tome 1 : Cartes. Etat des Lieux 2019 – Données 2012-2017. Report (Contract report). FRANCE. Available at: https://archimer.ifremer.fr/doc/00641/75280/.

Muller, A., Dubois, S.F., Boyé, A., Becheler, R., Droual, G., Chevalier, M., Pasquier, M., Roudaut, L., Fournier-Sowinski, J., Auby, I., Nunes, F.L.D., 2023. Environmental filtering and biotic interactions act on different facets of the diversity of benthic assemblages associated with eelgrass. Ecol. Evol. 13 (11), e10159. Available at: https://doi.org/10.1002/ece3.10159.

Nye, J.A., Baker, M.R., Bell, R., Kenny, A., Kilbourne, K.H., Friedland, K.D., Martino, E., Stachura, M.M., Van Houtan, K.S., Wood, R., 2014. Ecosystem effects of the Atlantic multidecadal oscillation. J. Mar. Syst. 133, 103–116. Available at: https://doi.org/10.1016/j.jmarsys.2013.02.006.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T. and Weedon, J. (2022) 'vegan: Community Ecology Package'.

Available at: https://CRAN.R-project.org/package=vegan (Accessed: 2 October 2022).

Peterson, C., Luettich, R., Micheli, F., Skilleter, G., 2004. Attenuation of water flow inside seagrass canopies of differing structure. Mar. Ecol. Prog. Ser. 268, 81–92. Available at: https://doi.org/10.3354/meps268081.

Poppeschi, C., Charria, G., Goberville, E., Rimmelin-Maury, P., Barrier, N., Petton, S., Unterberger, M., Grossteffan, E., Repecaud, M., Quéméner, L., Theetten, S., Le Roux, J.-F. and Tréguer, P. (2021) 'Unraveling salinity extreme events in coastal environments: a winter focus on the Bay of Brest', *Front. Mar. Sci.*, 8. Available at: https://doi.org/10.3389/fmars.2021.705403 (Accessed: 4 February 2023).

Quillien, N., Nordström, M., Gauthier, O., Bonsdorff, E., Paulet, Y., Grall, J., 2015. Effects of macroalgal accumulations on the variability in zoobenthos of high-energy macrotidal sandy beaches. Mar. Ecol. Prog. Ser. 522, 97–114. Available at: https://doi.org/10.3354/meps11151.

Quillien, N., Nordström, M.C., Le Bris, H., Bonsdorff, E., Grall, J., 2018. Green tides on inter- and subtidal sandy shores: differential impacts on infauna and flatfish. J. Mar. Biol. Assoc. U. K. 98 (4), 699–712. Available at: https://doi.org/10.1017/S0025315416002010.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ragueneau, O., Raimonet, M., Mazé, C., Coston-Guarini, J., Chauvaud, L., Danto, A., Grall, J., Jean, F., Paulet, Y.-M., Thouzeau, G., 2018. 'The impossible sustainability of the bay of Brest? Fifty years of ecosystem changes, interdisciplinary knowledge construction and key questions at the science-policy-community interface', *Frontiers in marine*. Science 5, 124. Available at: https://doi.org/10.3389/fmars.2018.00124.

Rao, C.R., 1964. The use and interpretation of principal component analysis in applied research. Sankhyā: Indian J. Stat. ser. A 329–358.

Rees, E.I.S., Nicholaidou, A., Laskaridou, P., 1977. 'The effects of storms on the dynamics of shallow water benthic associations', in *biology of benthic organisms*. Elsevier 465–474. Available at: https://doi.org/10.1016/B978-0-08-021378-1.50052-X.

Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: a global meta-analysis. Fish Fish. 19 (4), 698–715. Available at: https://doi.org/10.1111/faf.12283.

Silberberger, M.J., Renaud, P.E., Buhl-Mortensen, L., Ellingsen, I.H., Reiss, H., 2019. Spatial patterns in sub-Arctic benthos: multiscale analysis reveals structural differences between community components. Ecol. Monogr. 89 (1), e01325. Available at: https://doi.org/10.1002/ecm.1325.

Snelgrove, P.V.R., 1998. The biodiversity of macrofaunal organisms in marine sediments. Biodivers. Conserv. 7 (9), 1123–1132. Available at: https://doi.org/10.1023/A:1008867313340.

Snelgrove, P.V.R., Butman, C.A., 1994. Animal-sediment relationships revisited: cause versus effect. Oceanogr. Mar. Biol. Annu. Rev. 32, 111–177.

Soininen, J., 2014. A quantitative analysis of species sorting across organisms and ecosystems. Ecology 95 (12), 3284–3292. Available at: https://doi.org/10.1890/13-2228.1.

Solano-Barquero, A., Sibaja-Cordero, J.A. and Cortés, J. (2022) 'Macrofauna associated with a rhodolith bed at an oceanic island in the Eastern Tropical Pacific (Isla Del Coco National Park, Costa Rica)', *Front. Mar. Sci.*, 9. Available at: https://doi.org/10.3389/fmars.2022.858416 (Accessed: 17 October 2022).

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57 (7), 573–583. Available at: https://doi.org/10.1641/B570707.

Stockbridge, J., Jones, A.R., Gillanders, B.M., 2020. A meta-analysis of multiple stressors on seagrasses in the context of marine spatial cumulative impacts assessment. Sci. Rep. 10 (1), 11934. Available at: https://doi.org/10.1038/s41598-020-68801-w.

Thrush, S., Hewitt, J., Pilditch, C., Norkko, A., 2021a. Ecology of Coastal Marine Sediments: Form, Function, and Change in the Anthropocene, 1st edn. Oxford University Press. https://doi.org/10.1093/oso/9780198804765.001.0001. Available at:

Thrush, S.F., Hewitt, J.E., Cummings, V.J., Dayton, P.K., Cryer, M., Turner, S.J., Funnell, G.A., Budd, R.G., Milburn, C.J., Wilkinson, M.R., 1998. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. Ecol. Appl. 8 (3), 14.

Thrush, S.F., Hewitt, J.E., Gladstone-Gallagher, R.V., Savage, C., Lundquist, C., O'Meara, T., Vieillard, A., Hillman, J.R., Mangan, S., Douglas, E.J., Clark, D.E., Lohrer, A.M., Pilditch, C., 2021b. Cumulative stressors reduce the self-regulating capacity of coastal ecosystems. Ecol. Appl. 31 (1), e02223. Available at: https://doi.org/10.1002/eap.2223.

Toumi, C., De Cáceres, M., Grall, J., Boyé, A., Thiébaut, É., Maguer, M., Le Garrec, V., Broudin, C., Houbin, C., Gauthier, O., 2023. Long-term coastal macrobenthic community trajectory analysis reveals habitat-dependent stability patterns. Ecography 2023 (6), e06489. Available at: https://doi.org/10.1111/ecog.06489.

Turner, S.J., Hewitt, J.E., Wilkinson, M.R., Morrisey, D.J., Thrush, S.F., Cummings, V.J., Funnell, G., 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. Estuaries 22 (4), 1016. Available at: https://doi.org/10.2307/1353080.

Veiga, P., Redondo, W., Sousa-Pinto, I., Rubal, M., 2017. Relationship between structure of macrobenthic assemblages and environmental variables in shallow sublittoral soft bottoms. Mar. Environ. Res. 129, 396–407. Available at: https://doi.org/10.1016/j.marenvres.2017.07.002.

Watt, C.A., Scrosati, R.A., 2013. Bioengineer effects on understory species richness, diversity, and composition change along an environmental stress gradient: experimental and mensurative evidence. Estuar. Coast. Shelf Sci. 123, 10–18. Available at: https://doi.org/10.1016/j.ecss.2013.02.006.

WoRMS Editorial Board, . World Register of Marine Species. Available from. http://www.marinespecies.org. at VLIZ. Available at:. https://doi.org/10.14284/170.

Ysebaert, T., Herman, P., 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. Mar. Ecol. Prog. Ser. 244, 105–124. Available at: https://doi.org/10.3354/meps244105.