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Trait-based approach to monitoring marine benthic data along 500 km of coastline

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Abstract

Aim: β diversity and its linkages with ecosystem functioning remain poorly documented. This impedes our capacity to predict biodiversity changes and how they affect ecosystem functioning at scales relevant for conservation. Here, we address the functional implications of ongoing seafloor changes by characterizing at regional scale the taxonomic and functional α and β diversities of benthic habitats currently threatened by biotic homogenization.

Location: Western Europe.

Methods: Combining a trait-based approach to benthic community monitoring data covering a 7-year period and 500 km of coast, we explored the mechanisms governing community assembly in habitats associated with two types of foundation species, intertidal seagrass and subtidal maerl beds, compared to bare sediment at similar tidal level. We assessed their spatial and temporal variability and linked these mechanisms to their repercussions at regional scale through analyses of taxonomic and functional β diversity.

Results: Foundation species locally promote taxonomic and functional diversity. Maerl fine-scale heterogeneity promotes niche diversity and leads to high functional redundancy for the whole subtidal compartment, providing insurance for seafloor functioning. Seagrass high diversity seems more reliant on transient species and is associated with redundancy of only a few functions. Maintaining the seascapes in which seagrass are embedded seems essential to ensure their long-term functioning. At regional scale, the locally poorer bare sediment harbour similar functional richness as biogenic habitats because of higher within-habitat β diversity.

Main conclusions: Our study reinforces the conservation value of biogenic habitats but highlights that different mechanisms underlie their local diversity, which has implications for the vulnerabilities of their associated communities. Accounting for β diversity at regional scale also stressed a potential underrated conservation value of bare sediment for benthic ecosystem functioning. Coupling trait-based approaches to monitoring data can help link broad-scale β diversity to its underlying drivers,

bringing local mechanistic understanding closer to the scales at which biodiversity loss and management actions occur.

KEYWORDS
beta diversity, biotic homogenization, broad-scale monitoring, community assembly, coralline algae, ecosystem engineers, functional diversity, *Zostera marina*

1 | INTRODUCTION

Earth is profoundly marked by the imprints of anthropic activities (Steffen et al., 2011). In particular, anthropogenic impacts on natural ecosystems are causing a massive decline of biodiversity at global scale (Pimm et al., 2014). This imperils the functioning of ecosystems (Naeem, Duffy, & Zavaleta, 2012) and, thereby, the goods and services derived from them (Cardinale et al., 2012). Quantitatively, consequences of biodiversity loss on ecosystem functioning rival those of direct effects of global change stressors (Duffy, Godwin, & Cardinale, 2017; Hooper et al., 2012). Therefore, conservation policies should not account for biodiversity changes alone but should integrate consequences on ecosystem functioning and ecosystem services (Isbell et al., 2017). However, biodiversity-ecosystem functioning (BEF) relationships are currently best understood at fine spatial and temporal scales (Gamfeldt et al., 2015) and there is a growing consensus that measures of local diversity (α diversity, Whittaker, 1960) cannot fully capture current biodiversity trends (Hillebrand et al., 2017). Patterns of biodiversity changes are scale-dependent, being more pervasive and consistent at broader spatial scales (Jarzyna & Jetz, 2018; McGill, Dornelas, Gotelli, & Magurran, 2015). There is thus a mismatch between our fine-scale understanding of BEF relationships and the broad scales of anthropogenic stressors and conservation policies (Isbell et al., 2017).

Despite the large consensus that local diversity loss threatens ecosystem functioning (Cardinale et al., 2012), current changes might not systematically impact α diversity (Hewitt, Thrush, Lohrer, & Townsend, 2010; Primack et al., 2018). Indeed, constant α diversity may hide substantial changes in community composition and structure in space and time (β diversity, Whittaker, 1972; Dornelas et al., 2014) and understanding them is critical to determine how local changes scale-up at broader scales (Socolar, Gilroy, Kunin, & Edwards, 2016). Anthropogenic stressors are known to reduce β diversity at broad scale (Socolar et al., 2016). This "biotic homogenization" appears as the main component of biodiversity loss worldwide (Olden & Rooney, 2006; Primack et al., 2018) and is increasingly recognized as a critical threat for ecosystem functioning (Hautier et al., 2017; Plas et al., 2016) and resilience (Isbell et al., 2018). Yet, β diversity and its underlying drivers remain poorly documented (McGill et al., 2015) and its links with ecosystem functioning have received little attention compared to those of α diversity (Mori, Isbell, & Seidl, 2018). It is necessary to fill these knowledge gaps to better understand and predict the consequences of biodiversity changes at broad scales (Burley et al., 2016; Mori et al., 2018).

Species influences on ecosystem properties and their responses to their environment are mediated by physiological, morphological, phenological and behavioural characteristics, so-called functional traits (Violle et al., 2007). Trait-based approaches offer an integrative framework to apprehend both the causes and functional consequences of biodiversity changes (Suding et al., 2008) and scale-up our understanding of BEF relationships (Burley et al., 2016; Violle, Reich, Pacala, Enquist, & Kattge, 2014). It has been shown that taxonomic and functional (trait-based) β diversity may be spatially decoupled and cannot serve as reciprocal proxies (Devictor et al., 2010; Loiseau et al., 2016). As such, while temporal changes in functional β diversity may track taxonomic variation (Brice, Pellerin, & Poulin, 2017; Naaf & Wulf, 2012), functional homogenization can exceed the extent of taxonomic homogenization (Mori et al., 2015; Villéger, Grenouillet, & Brosse, 2014) while in other instances, changes in species assemblages occur with no effect on functional composition (Sonnier, Johnson, Amatangelo, Rogers, & Waller, 2014; White, Montgomery, Storchová, Hořák, & Lennon, 2018). As the functional outcomes of biotic homogenization remain largely underexplored (Olden, Comte, & Giam, 2018), there is an urgent need to disentangle the links between species susceptibility and their role in ecosystem functioning and resilience to understand when and where species changes might have the largest impact (Bracken, Friberg, Gonzalez-Dorantes, & Williams, 2008; Oliver et al., 2015). In this respect, consequences of habitat degradation on ecosystem functioning have received increasing attention in terrestrial ecosystems (Liu et al., 2018). Parallel issues face marine benthic systems (Snelgrove, Thrush, Wall, & Norkko, 2014). Yet, data remain scant and further research is needed (Mazor et al., 2018).

Benthic communities are essential for the functioning of coastal ecosystems (Snelgrove et al., 2014) that face increasing anthropogenic pressures and rank amongst the most impacted ecosystems worldwide (Halpern et al., 2015). The most diverse and productive coastal habitats, such as seagrasses, macroalgae and biogenic reefs, are particularly threatened (Airoldi & Beck, 2007). These biogenic habitats, formed by ecosystem engineers (Jones, Lawton, & Shachak, 1994), are acutely vulnerable to environmental changes (Airoldi & Beck, 2007). The degradation of foundation species (sensu Dayton, 1972) populations imperils the high local and among-habitat diversities they create (Airoldi, Balata, & Beck, 2008). Additionally, space–time variability of ecosystem engineer's effects on diversity (Crain & Bertness, 2006) can lead to high within-habitat β diversity (Boyé, Legendre, Grall, & Gauthier,

2017). However, current understanding of biogenic habitats diversity is mostly local and focused on taxonomic diversity (Romero, Gonçalves-Souza, Vieira, & Koricheva, 2015), and their contribution to within- and among-habitat β diversity, as well as the functional facet of their associated diversity, is rarely considered (Airoldi et al., 2008). This leaves great uncertainties in predicting the consequences of their broad-scale degradation (Snelgrove et al., 2014).

Here, we focus on the role of two biogenic habitats, intertidal *Zostera marina* meadows (Figure 1d) and subtidal maerl beds (unattached coralline red algae) formed by at least two species: *Lithothamnion corallioides* and *Phymatolithon calcareum* (Riosmena-Rodríguez, Nelson, & Aguirre, 2017; Figure 1e). These biogenic habitats are under substantial threats worldwide (Grall & Hall-Spencer, 2003; Waycott et al., 2009). To better apprehend the potential consequences of their degradation, we compare their taxonomic and functional α and β diversities to those of bare sediment using monitoring data covering three years (2007, 2010 and 2013) and the whole Brittany seaboard (France; Figure 1a), a highly diverse environmental mosaic (Boyé et al., 2017). For this purpose, we develop a trait-based approach focused on *Polychaeta* (Phylum Annelida), a phylogenetically diverse class comprised of a great diversity of species exhibiting a wide range of ecological strategies (Giangrande, 1997; Jumars, Dorgan, & Lindsay, 2015) and having a critical role in ecosystem functioning through activities such as bioturbation (Queirós et al., 2013). In a first part, we explore the mechanisms governing species coexistence in these different habitats and the variability of these mechanisms in space and time, with the hypothesis that the facilitative effects of foundation species would reduce the imprint of abiotic constraints on benthic communities (Bulleri et al., 2018) and lead to more constant community assembly in biogenic than in bare sediment. In a second part, we address how these mechanisms scale-up by assessing how each habitat contributes to taxonomic and functional diversity at the regional scale. We hypothesize that the facilitative effects of foundation species should promote higher α diversity (Romero et al., 2015) but at the expense of a lower β diversity within biogenic than bare sediment, due to more constant assembly mechanisms. The balance of these two processes is however difficult to predict, leading to uncertainties regarding the contribution of each habitat to regional diversity.

2 | METHODS

2.1 | Field sampling

In the context of the ongoing REBENT (*Réseau Benthique*) monitoring programme (2003-present; http://www.rebent.org), 50 benthic communities were monitored yearly across 42 sites spanning the Brittany seaboard (Figures 1a and S1), representing four habitats: 9 intertidal seagrass beds and 9 subtidal maerl beds for the biogenic habitats, 18 intertidal sandy beaches and 14 locations of subtidal

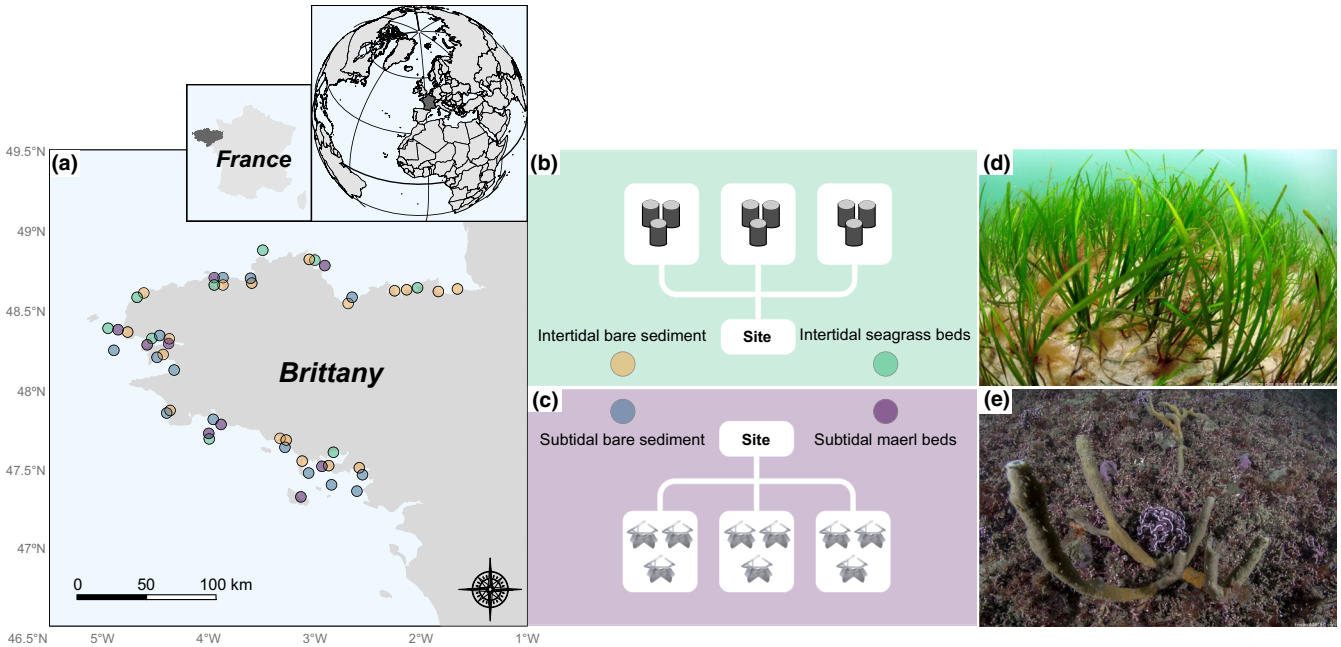

FIGURE 1 (a) Map of the monitored sites. (b) For intertidal habitats, three points are sampled at each site using three sets of three sediment cores, each cylinder representing one such set. (c) For subtidal habitats, three points are sampled at each site using three Smith-McIntyre grabs. The nine cores or grabs were then pooled to estimate abundances at the site level. Accordingly, macrofaunal densities were estimated based on 0.27 m^2 and 0.9 m^2 surfaces sampled per site for the intertidal and subtidal sites, respectively. (d) Photography of a *Zostera marina* meadow; photography credit: Yannis Turpin, Agence des aires marines protégées. (e) Photography of a maerl bed; photography credit: Erwan Amice, Centre National de la Recherche Scientifique (CNRS)—Laboratoire des sciences de l'Environnement MARin (LEMAR)

TABLE 1 Traits and modalities used in this study along with their abbreviations in Figure 5

Trait	Modalities	Abbreviations
Maximum size (mm)	<2	Size_inf2
	2–5	Size_2–5
	5–10	Size_5–10
	10–50	Size_10–50
	50–100	Size_50–100
	100–200	Size_100–200
	>200	Size_sup200
Feeding method	Subsurface deposit feeder	SSDF
	Surface deposit feeder	SDF
	Active suspension feeder	ASF
	Passive suspension feeder	PSF
	Grazer	Grazer
	Predator	Pred
	Scavenger	Scav
	Parasitic	Parasitic
Food size	Microphagous	Microphagous
	Macrophagous	Macrophagous
Adult preferred substrate position	Infaunal	Infaunal
	Epibenthic	Epibenthic
Living habit	Tube dweller	Tube_dweller
	Burrower	Burrower
	Crawler	Crawler
	Swimmer	Swimmer
	Attached	Attached
Daily adult movement capacity	None (0 m)	Mob_0
	<10 m	Mob_inf10
	10–100 m	Mob_10–100
	100–1,000 m	Mob_100–1000
Bioturbation	None	Bioturb_N
	S Surficial modifiers	Bioturb_S
	B Biodiffusors	Bioturb_B
	UC Upward conveyors	Bioturb_UC
	DC Downward conveyors	Bioturb_DC
	R Regenerators	Bioturb_R
Sexual differentiation	Hermaphrodite	Hermaphrodite
	Gonochoric	Gonochoric
Development mode	Asexual	Dev_asex
	Direct	Dev_direct
	Indirect—planktotrophic	Dev_plankto
	Indirect—lecithotrophic	Dev_lecitho
Reproduction frequency	Iteroparous	Iteroparous
	Semelparous	Semelparous
Life span	Short (<2 years)	Short_life_span
	Medium (2–5 years)	Medium_life_span
	Long (>5 years)	Long_life_span

sediment devoid of biogenic habitats (respectively referred to as intertidal and subtidal bare sediment thereafter). These locations were chosen to encompass within each habitat most of the environmental settings found along Brittany's coasts (Boyé et al., 2017; Quillien, Nordström, Guyonnet, et al., 2015), although the extent of the environmental variability covered within each habitat may slightly vary (Figure S2). Thereafter, the term *site* refers to a given habitat in a given location. The terms *observation* and *assemblage*, respectively, refer to a sampling occasion at a given site in a given year and to the polychaete composition for this observation.

This study focuses on three years of the REBENT monitoring programme (2007, 2010 and 2013), chosen to maximize the spatial and temporal coverage of the data while ensuring similar temporal resolution for all sites (see Figure S1). Sampling was performed for all sites between the end of February and the beginning of May, before the recruitment of most species (Dauvin, Ruellet, Desroy, & Janson, 2007), using a standardized protocol summarized in Figure 1b,c (details in Appendix S1). Note that sampling gears differ between intertidal and subtidal sites so that comparisons are fully meaningful within a given tidal level, while comparisons between two tidal levels may bear methodological imprint.

2.2 | Trait collection

For the purpose of this study, we focused on the 234 observed Polychaeta. We collated data for 10 traits, divided into a total of 41 categories. These traits characterized maximum size, feeding and reproductive ecology, mobility and bioturbation potential of the species (Table 1) and were chosen to reflect key biological and ecological processes (Table S1). Trait data were collected from the publicly available database Polytraits (http://polytraits.lifewatchgreece.eu), reviews on the reproduction and feeding ecology of polychaetes (Giangrande, 1997; Jumars et al., 2015; Rouse & Pleijel, 2006) and on bioturbation potential (Queirós et al., 2013), primary literature on specific species or genera, or from expert knowledge. Information was collected at the lowest possible taxonomic level and inferred when missing from data available from other species in the genus, or in the most extreme cases, in the same family (feeding-related and mobility traits only and for families showing low variability for these traits). For reproduction frequency, development mode and sexual differentiation, data were missing for 9% (21), 7% (17), and 1% (3) of the species, respectively, and were imputed (Appendix S1). Species were scored for each trait modality based on their affinity using a fuzzy coding approach (Chevenet, Dolédec, & Chessel, 1994). The coding procedure, detailed in the Appendix S1, allowed for the incorporation of within-species variability.

The observation-by-trait matrix containing the total abundances of each modality within the assemblages was calculated using the matrix product of the observation-by-species matrix (usually referred to as site-by-species), containing the abundances of the species in the assemblages, with the filled species-by-trait matrix, containing the relative expression of trait modalities by species after

standardization of the scores to 1 per trait and per species. This procedure partitions, for each trait, the abundances of the species into the different modalities they expressed. For example, if an assemblage contains a single species with 10 specimens and this species is indifferently predator and scavenger (therefore coded 0.5 for both modalities after standardization), this assemblage has 5 predators and 5 scavengers in the assemblage-by-trait matrix. In this matrix, the sum of each trait for an observation is the total abundance of the species found in the assemblage.

2.3 | Data analyses

Indices describing complementary aspects of taxonomic and functional α diversity were used to explore among habitats differences in assemblages. In addition to total abundance and species richness, taxonomic diversity was characterized by the Simpson diversity index, calculated as (Greenberg, 1956):

$$D = 1 - \sum_{i=1}^{S} p_i^2$$

with S being the species richness of the assemblage and p_i the relative abundance of species i. This index was used because of its relationship with Rao's quadratic entropy (Rao, 1982) used to measure functional diversity in the null model developed below. It is a specific case of Rao's index where all species are considered maximally different from each other (Botta-Dukát, 2005). Simpson's index also has the desirable property of down-weighting rare species (Hill, 1973) that may not have been properly sampled in such a monitoring programme. The functional structure of assemblages was characterized using four indices: *functional richness* (FRic), *functional evenness* (FEve), *functional divergence* (FDiv) and *functional dispersion* (FDis, Laliberté & Legendre, 2010; Villéger, Mason, & Mouillot, 2008). These indices are complementary and together depict different facets of the functional structure of communities (Mouchet, Villéger, Mason, & Mouillot, 2010). They are defined and described in more details in Appendix S1.

We used a null model approach to assess whether observed functional diversity of assemblages matched that expected when community assembly is independent of species traits, and evaluate how biogenic habitats may influence assembly mechanisms. Rao's quadratic entropy, adequate for detecting trait convergence and divergence (Botta-Dukát & Czúcz, 2016), was computed for each assemblage. We then compared observed values to those of simulated communities to assess the prevalence of trait divergence (higher diversity than expected), convergence (lower diversity than expected) or random distribution among the assemblages of each habitat (Perronne, Munoz, Borgy, Reboud, & Gaba, 2017). Simulations were run with all traits simultaneously and for each trait separately, to account for assembly processes that might act contrastingly on different traits (Spasojevic & Suding, 2012). Randomizations of the site-by-species matrices were restricted within tidal levels, that is species could move freely between biogenic and bare habitats within a tidal level but not across intertidal and subtidal assemblages. The randomization procedure was constrained to keep constant: (a) assemblage species richness, (b) species occurrences (number of samples where a species occurs) at the regional scale and within each tidal level and (c) total abundance of each species at the regional scale and within each tidal level. This procedure was implemented using the *trial-swap* method of the *randomizeMatrix* function from the PICANTE R package (Kembel et al., 2010) and was used to simulate 1,000 randomly assembled communities. For each simulation, 100,000 trial swaps were done. Standard Effect Size (SES, Gotelli & McCabe, 2002) for each community was used to compare observed values and null models outputs:

$$\mathrm{SES} = \frac{RaoQ_{\mathrm{observed}} - \mu_{\mathrm{nullmodels}}}{\sigma_{\mathrm{nullmodels}}}$$

with $\mathrm{RaoQ}_{\mathrm{observed}}$ the observed functional diversity, $\mu_{\mathrm{nullmodels}}$ the mean of the null distribution of the functional diversity, and $\sigma_{\mathrm{nullmodels}}$ its standard deviation. Positive SES values indicate trait divergence whereas negative values suggest trait convergence. Near-zero values indicate random distribution.

Taxonomic and functional β diversities were visualized using principal component analysis (PCA) of the Hellinger-transformed species and trait modality abundances. Hellinger transformation allows for the use of Euclidean-based methods on frequency data and has the desirable property of not giving excessive weight to rare species (Legendre & Gallagher, 2001). The extent of within-habitat regional β diversity was quantified using the overall variance of the Hellinger-transformed assemblage-by-species and assemblage-by-modalities matrices (BDtot) as proposed by Legendre and De Cáceres (2013). Again, these values of BDtot are only comparable within tidal levels due to the previously raised methodological constraints. BDtot values were then put in relation to the contribution of each habitat to regional functional richness. The latter was assessed through habitat percentage occupancy of the regional trait space, calculated as the convex hull volume occupied by the species of one or several assemblages, divided by the global convex hull, defined as the volume (functional richness) of the species-by-trait matrix containing all species found over the whole study (all sites and the three years of data; McWilliam et al., 2018). The relative contribution of α and β diversities of each habitat to regional functional richness was assessed by comparing the average contribution of the assemblages of the habitats (volume occupancy of the species found in each assemblage) to the total contribution of the habitats at the regional scale (volume occupancy of all the species found within each habitat over the whole study). Lastly, the relationships between taxonomic and functional β diversity patterns were assessed using coinertia analyses (Dolédec & Chessel, 1994) between the PCA of Hellinger-transformed species and trait abundances, both within each habitat, and across all samples. The RV coefficient (Robert & Escoufier, 1976), a multivariate generalization of the squared Pearson's correlation (Legendre & Legendre, 2012), was used to quantify these relationships.

All statistical analyses were performed using R (R Core Team, 2017). Simpson diversity and Rao's quadratic entropy were calculated using the *rao.diversity* function of the SYNCSA package (Debastiani & Pillar, 2012). FRic, FEve, FDiv, and FDis were calculated using the *dbFD* function of the FD package (Laliberté, Legendre, & Shipley, 2014). All other analyses relied on the VEGAN package (Oksanen et al., 2017).

3 | RESULTS

3.1 | Taxonomic α and β diversities

The main gradient in polychaete taxonomic β diversity, materialized by the first PCA axis (Figure 2), separates bare sediment assemblages (left) from those from biogenic habitats (right). These differences account for more than 14% of the total variance and surpass those separating intertidal from subtidal assemblages, reflected partly on the second PCA axis and for which it is impossible to separate ecological from sampling gear-related variation. Differences between biogenic and bare habitats assemblages emerged irrespectively of sampling methods. This supports a strong structuring effect of foundation species on polychaete assemblages. Nonetheless, some overlap between bare and seagrass habitat is observed in the intertidal, highlighting variability in the extent of this effect. This overlap mostly involves sites where bare and seagrass communities were monitored a few metres apart, bare sediment assemblages being more similar to their neighbouring seagrass beds than to the other bare sediment assemblages of the region (Figure S3).

Biogenic habitats have conspicuous effects on the α diversity of polychaete assemblages (Figure 3). They consistently increased species richness within tidal levels, while differences in abundance or Simpson diversity were less consistent and of lesser extent. Harbouring from 32 to 73 species each, with an average of 53 species (±2.1; Standard Error [*SE*]), maerl beds hosted, by far, the richest assemblages. With 6 to 68 species and an average of 29 (±2.2; *SE*), subtidal bare sediment appeared locally poorer. Intertidal seagrass meadows, with 10 to 50 species and an average of 25 species (±1.7; *SE*), hosted a similar richness as subtidal bare sediment and richness higher than intertidal bare sediment that harboured only 1–29 species, with an average of 12 species (±1.0; *SE*). Abundance on the other hand was on average higher in subtidal bare sediment than in maerl beds and also higher in intertidal seagrass meadows than in intertidal bare sediment. This was mostly due to a higher variability and extreme values in subtidal bare sediment and intertidal seagrass meadows. Simpson diversity did not show major differences among habitats within tidal levels.

3.2 | Functional α diversity

The positive effect of biogenic habitats on species richness within tidal levels translated into higher functional richness values for

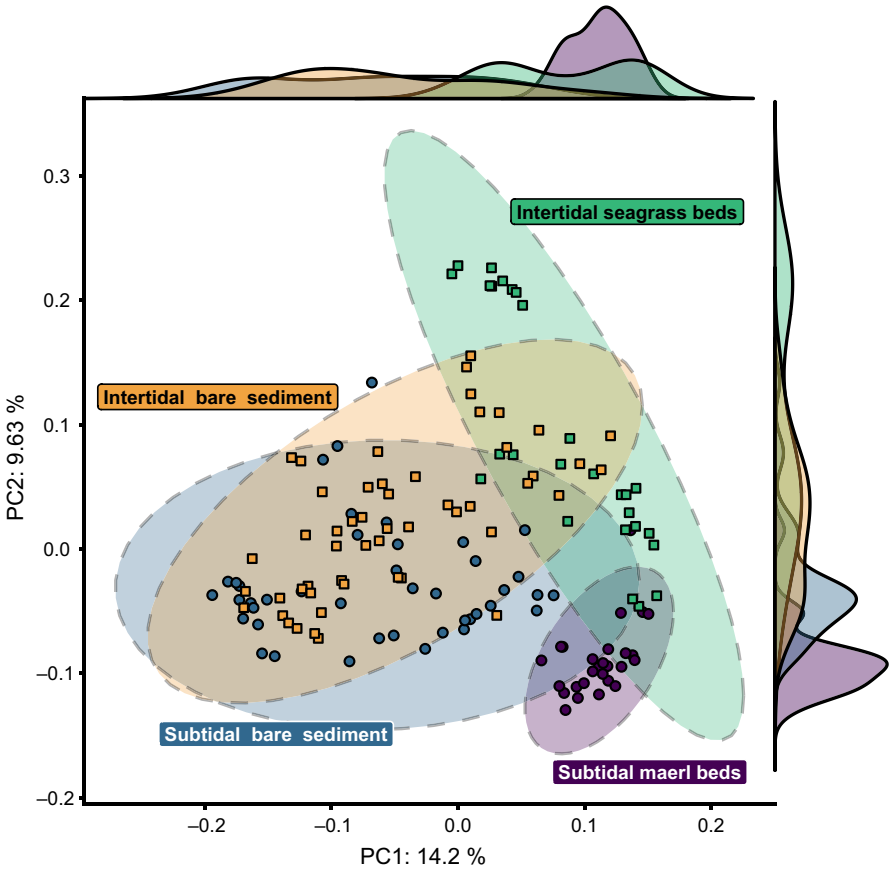

FIGURE 2 Principal component analysis of Hellinger-transformed polychaete abundances. Samples are displayed in scaling 1 in the central panel. The shapes of the points reflect differences in the tidal levels and sampling methods: squares represent intertidal habitats sampled using sediment cores and circles represent subtidal habitats sampled using Smith-McIntyre grabs (see Figure 1). The densities of points for each habitat along the first and second axis are displayed as curves in the outer panels. Within-habitat variability comprises of both spatial and temporal variations (see Figure S1). The first two principal component analysis axes represented account together for 23.83% of the total variance of Hellinger-transformed polychaete composition. The species scores associated with this analysis are represented in Figure S7

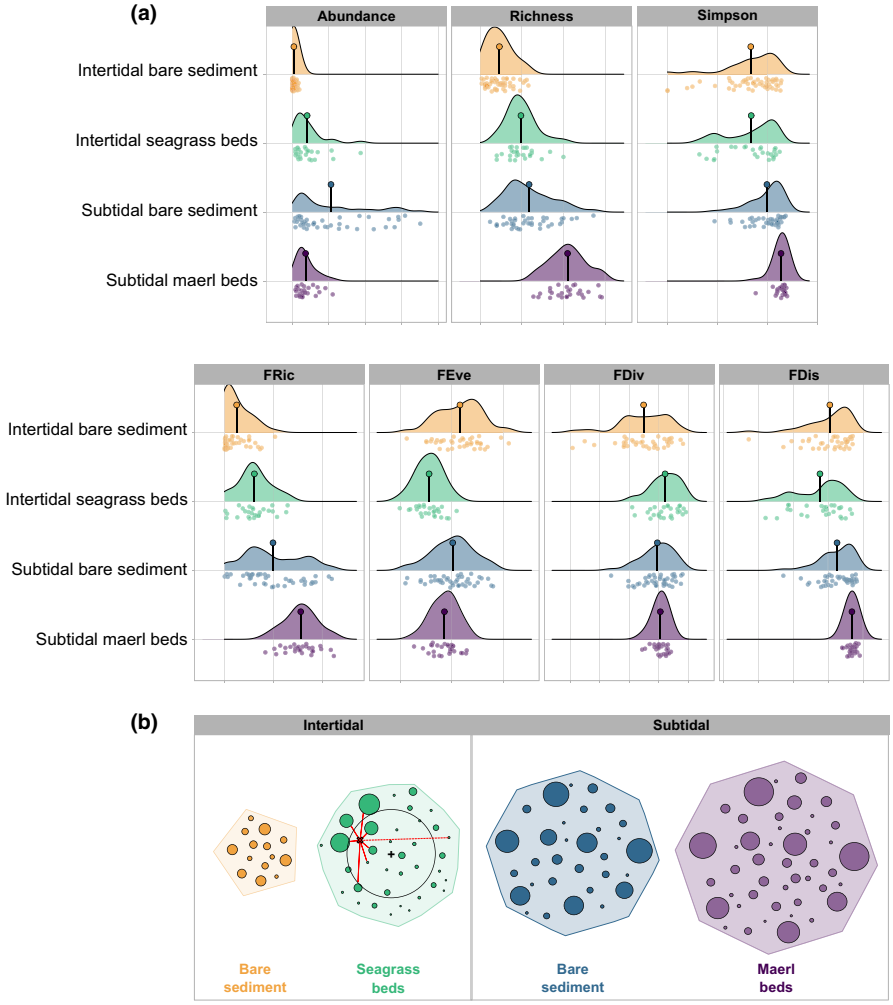

FIGURE 3 (a) Distribution of taxonomic and functional α-diversity indices among the four habitats. (b) Schematic view derived from these indices of the functional spaces representing an average assemblage of each habitat. (a) For each habitat, the distributions include the values of the different sampled sites with, for each site, values for the 3 years (2007, 2010, 2013). The mean value for each of these indices is represented by the point pinned on each distribution. Abundance corresponds to the total abundance of each assemblage (one site for one habitat at 1 year). Richness corresponds to the species richness of the assemblage. Simpson corresponds to Simpson's diversity index. FRic, FEve, and FDiv correspond to the functional richness, the functional evenness and the functional divergence, respectively, and were calculated on 5 PCOA axis representing 66% of the original species dissimilarity matrix. FDis corresponds to the functional dispersion. (b) Conceptual representation of species abundances in functional space (following representations from Boersma et al., 2016; and Mouillot, Graham, Villéger, Mason, & Bellwood, 2013) integrating the insights provided by the different functional indices (see Appendix S1: Section *Description of the functional indices and their complementarity*) to depict the functional structure of a typical assemblage of each of the four habitats. Circle size reflects the relative abundance in each trait space of each particular traits combination. The convex polygons represent in two dimensions the volume of the trait space, larger surfaces representing higher FRic. The centre of gravity of the functional space (black cross) and the abundance-weighted centroid (red cross) are schematically represented for the seagrass trait space to illustrate our conceptual explanation for how lower functional dispersion than in bare sediment can emerge despite higher FRic and FDiv. The black circle represents the hypothetic mean functional distance from the centre of gravity. It is high if all abundant species are found at the extreme part of the trait space, as in the representation where all are clustered on the edge of the trait space. The red dotted lines represent the distances of some species to the abundance-weighted centroid. All distances are weighted by abundances and averaged in the calculation of FDis. Therefore, FDis can be low despite high FRic and FDiv if, as represented, the abundance-weighted centroid is close to the abundant species when these are all clustered together at the edge of the trait space and if all species far from the centroid are rare and have therefore low weights in the averaging of the distances during the calculation of FDis

seagrass and maerl beds (Figure 3a; FRic). Other facets of functional diversity were affected differentially. In subtidal environments, maerl and bare sediment-associated assemblages displayed similar average functional evenness (Figure 3a; FEve), functional divergence (Figure 3a; FDiv) and functional dispersion (Figure 3a; FDis). The spatial and temporal variability of these indices, however, differed between the two subtidal habitats, with more stable values found in maerl beds (less dispersed distributions). In contrast, seagrass meadows deeply modified the functional α-diversity profiles of intertidal assemblages, decreasing functional evenness and, to

a lesser extent, functional dispersion, while increasing functional divergence.

To summarize the results provided by the α diversity indices, the functional structure of a typical assemblage of each habitat was derived from the different taxonomic and functional indices and schematized in Figure 3b. A typical assemblage in intertidal bare sediment has a species-poor and small functional space (low FRic) with evenly distributed abundances (high FEve). In comparison, seagrass promotes broader functional spaces (higher FRic) where abundances are clustered (low FEve) with higher abundances gathered at the edges of trait space (high FDiv). This indicates that dominant species share similar characteristics that are fairly different from all other species (mainly microphagous suspensive and deposit feeders and sessile tube builders, see result section 3.4) and that a large part of trait space is occupied by rare species with rare traits. In subtidal areas, maerl hosts more species and promotes broader functional spaces (higher FRic and FDis) than bare sediment but within these functional spaces, abundances are distributed in a similar fashion (similar FEve and FDiv).

3.3 | Assembly mechanisms: trait convergence/divergence

Comparing observed functional diversity to null expectations (Figure 4) revealed differences in assembly mechanisms between biogenic and bare habitats, but also between the two biogenic habitats (Figure 4a). First, in bare sediment, and irrespective of tidal level, SES values appeared highly variable in both space and time (Figure 4a,b), a pattern also found when considering traits individually (Figure S4). Standard Effect Size varied from highly positive, that is higher functional diversity than expected, reflecting

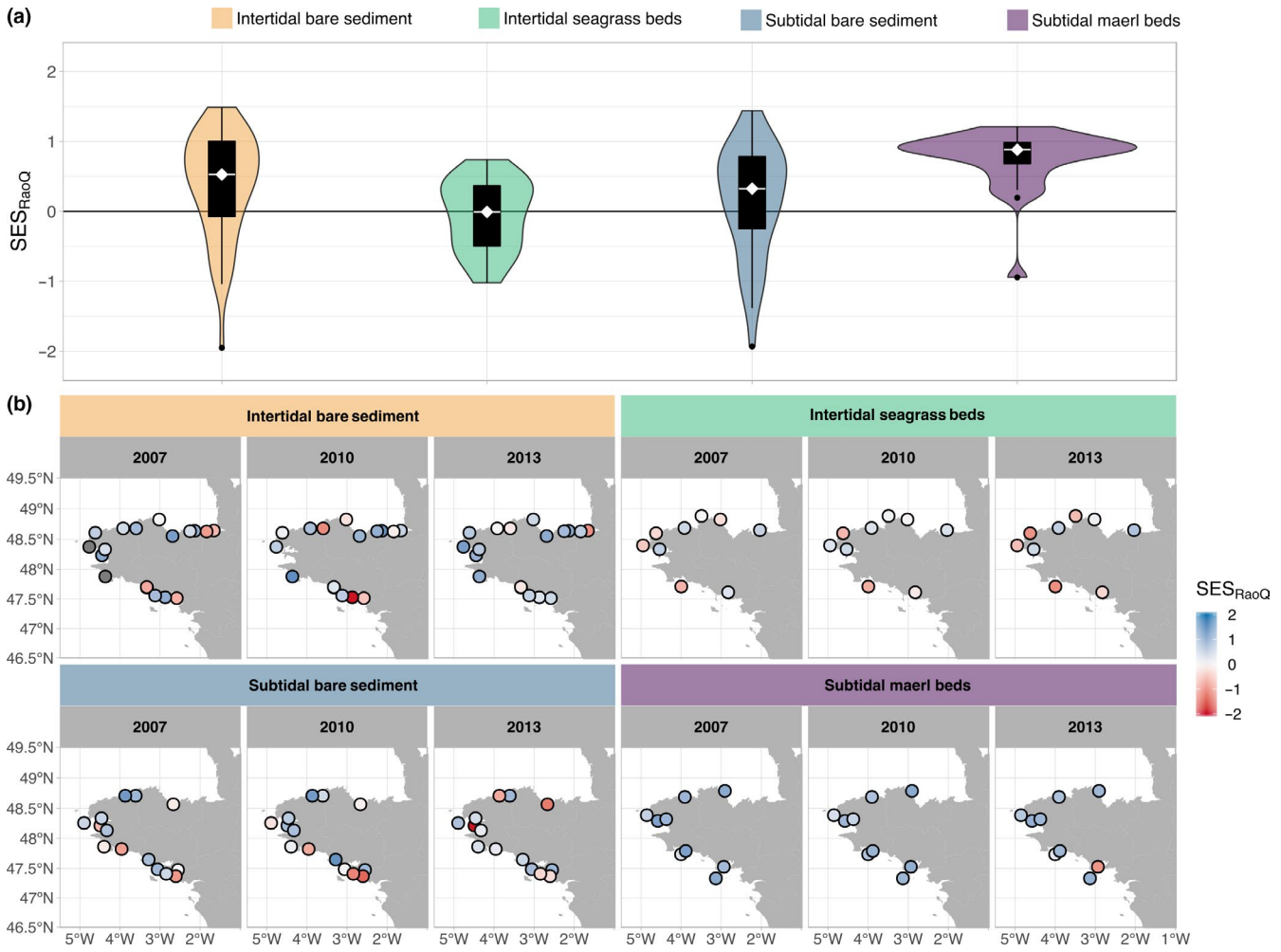

FIGURE 4 (a) Distribution of the Standard Effect Size (SES) values within each habitat. (b) Maps of the spatial distribution of SES values for each habitat and for the three years. Positive SES values indicate trait divergence and negative values trait convergence. Values near zero indicate random distribution. We did not test for the significance of each individual value as our interest lied in characterizing the distribution of SES values at the scale of the four habitats. Nonetheless, note that SES values below −1.96 or higher than 1.96 are often interpreted as being statistically significant with the implicit assumption that z-ratios follow a normal distribution (Veech, 2012). However, normality of the null distributions was not verified here. Dark grey dots in 2007 for intertidal bare sediment corresponds to two samples with only one species. Hence, for these samples RaoQ diversity is 0 and SES values cannot be calculated because the richness of the sites are kept constant in the trial-swap model, always giving a functional diversity of 0 for these sites

strong trait divergence, to highly negative, that is lower functional diversity than expected, reflecting strong convergence, through near-zero values, not departing from the null models. Notably, the assemblages with the highest trait divergences in intertidal bare sediment were those with the lowest abundances and species richness within this habitat while these two factors appeared unrelated to the SES values within subtidal bare sediment (Figure S5). Comparatively, both biogenic habitats SES values were more stable but, as previously observed for the functional indices, the two types of engineers differed in their signatures (Figure 4a). Maerl beds assemblages consistently displayed higher functional diversity than expected (Figure 4b), as did each individual trait with the exception of reproduction frequency (Figure S4) whose convergence seems linked to the high dominance of iteroparous species and the consistently low abundance of semelparous polychaetes in maerl assemblages (Figure S6). In comparison, SES values of seagrass assemblages were confined between −1 and 1, trait dispersion matching with random expectations. Standard Effect Size values for both maerl and seagrass bed assemblages appeared unrelated to abundance and richness (Figure S4). In summary, SES values revealed extremely variable assembly mechanisms in bare sediment and more stable ones in biogenic habitats. Furthermore, the two biogenic habitats acted differentially on trait dispersion, with seagrass assemblages consistently matching with null expectations and maerl beds promoting trait divergence, irrespectively of the location and underlying environment.

3.4 | Functional β diversity

The greater variability of local assembly mechanisms in bare sediment translates into greater taxonomic and functional β diversities in these habitats (BDtot, Table 2). The twofold increase in functional BDtot in bare sediment is also apparent on the first two axes of the trait-based PCA (Figure 5). At regional scale, these high taxonomic and functional β diversities compensate for the lower local diversity of these assemblages as, within tidal levels, bare habitats harbour a similar regional functional richness as their biogenic counterparts (Total occupancy of regional trait space; Table 2). Intertidal and subtidal bare sediment assemblages, respectively, cover 62% and 82% of the regional functional space, that is that formed by all species found in this study. In comparison, seagrass and maerl beds assemblages, respectively, cover 64% and 86% of this space. However, different patterns underlie these values: on average, a single intertidal bare sediment assemblage covers one-third of the functional space occupied by a seagrass meadow, and a subtidal bare sediment assemblage covers half the space of a maerl bed (Average occupancy; Table 2). Although there are some quantitative differences in the contribution of each habitat, in particular for subtidal bare sediment, taxonomic richness behaves in the same way (Table 2).

The PCA of trait composition illustrates how bare and biogenic habitats can reach similar regional functional richness (Figure 5). Indeed, the centroids for both subtidal habitats and for intertidal bare sediment assemblages are located near the origin of PCA space, indicating that all modalities are equivalently represented in these assemblages at the regional scale. This is confirmed by the third and fourth PCA axes (not shown). However, all maerl assemblages are located near the origin, stressing that each of these assemblages is functionally rich and harbours all the modalities relatively equivalently. On the other hand, intertidal bare sediment assemblages are extremely variable in their trait composition, from assemblages with high proportions of mobile macrophagous predators and scavengers with mostly biodiffusing actions on the sediment (on the left of the PCA) to assemblages with opposite characteristics, dominated by sessile microphagous suspensive and deposit feeders (on the right), through assemblages dominated by large active suspension feeders and by species with planktotrophic development which mainly modify

TABLE 2 Variability of species and trait community compositions within each habitat at regional scale, in relation to the proportion of regional functional space and species richness found in each habitat, either on average per assemblage, or in total at regional scale. Within-habitat β diversity was measured using the total variance of the observation-by-species matrix of each habitat (termed BDtot for total β diversity, sensu Legendre & De Cáceres, 2013), both in terms of species (Taxonomic BDtot) and trait composition (Functional BDtot). The percentage of occupancy of the regional multidimensional trait space was measured based on the first 6 axes of the PCA of the species-by-trait matrix, which contained 70.36% of total variance. It was calculated as the percentage of the volume formed by all the species found in this study (regional richness) that is represented by the volume formed by all the species found in each habitat at the regional scale, considering all sites and all years (total occupancy), or by the volume formed by all the species found in each assemblage, which was then averaged per habitat (average occupancy ± standard deviation [*SD*]). The same approach was applied for the taxonomic richness of polychaete species with the percentage of the regional species pool found in each habitat, in total and on average per assemblage

Habitat	Taxonomic BDtot	Functional BDtot	Total occupancy of regional trait space (%)	Average occupancy of regional trait space (%) ± *SD*	Total contribution to regional taxonomic richness (%) ± *SD*	Average contribution to regional taxonomic richness (%) ± *SD*
Intertidal bare sediment	0.75	0.13	61.77	2.76 ± 4.02	40.20	4.96 ± 3.21
Intertidal seagrass beds	0.52	0.06	64.14	9.34 ± 6.52	47.00	10.50 ± 3.83
Subtidal bare sediment	0.60	0.06	82.27	15.67 ± 12.88	60.30	12.60 ± 6.16
Subtidal maerl beds	0.47	0.03	86.10	28.24 ± 7.93	77.80	22.40 ± 4.67

the surficial sediment layers (bottom of the ordination plot). Taken together, these local functional assemblages express all modalities in intertidal bare sediment at the regional scale. Subtidal bare sediment assemblages are intermediate with functionally rich local assemblages and intermediate dispersion, as previously shown by the BDtot values (Table 2). Seagrass assemblages, on the other hand, display a different and more internally consistent and specialized trait signature with positions shifted on the first axis towards higher relative proportions of microphagous suspensive and deposit feeders and sessile tube builders. In particular, and in contrast with intertidal bare sediment, seagrass assemblages also tend to be dominated by species with similar sediment reworking activities, either upward- or downward conveyors. Seagrass assemblages are also characterized by a lower relative proportion of macrophagous mobile predators and scavengers. Therefore, in contrast with the other habitats, seagrass assemblages have a clear and consistent trait signature.

3.5 | Relationships between taxonomic and functional β diversity

Overall, the within- and among habitats taxonomic β diversity (Figure 2) differ from functional β diversity (Figure 5) and the RV coefficient (RV = 0.62) reflected this (Figure 6). The strength of the taxonomy–trait composition relationship varies among habitats: it is rather strong in seagrass beds (RV = 0.85) and subtidal bare sediment (RV = 0.71), while it is fairly weak in intertidal bare sediment (RV = 0.56) and maerl beds (RV = 0.54). Multivariate dispersion of seagrass assemblages is indeed nearly identical in both spaces, and differences are slight for subtidal bare sediments (Figure 6). In contrast, intertidal bare sediment assemblages are more dispersed in trait than in taxonomic space (Figure 6), with functional BDtot 1.5 to 4 times that observed elsewhere (Table 2). Maerl assemblages display similar dispersions in both spaces, confirming their high taxonomic and functional stability (Figure 6; Table 2). However, this is the only habitat for which there seems to be a shift in centroid position—rather than dispersion (Figure 6). This illustrates a taxonomy–trait decoupling with maerl assemblages differing from other habitats more in terms of taxonomy than traits, as illustrated by their relative position in the taxonomic (Figure 2) and trait-based (Figure 5) ordinations.

4 | DISCUSSION

4.1 | Processes underlying local diversity and influence of biogenic habitats

Trait distributions within communities provide key insights into the assembly mechanisms underlying species diversity (Perronne et al., 2017). In this respect, SES value's high variability in bare sediment suggests important variation in the relative strength of abiotic and biotic constraints across this environmentally heterogeneous region. Trait convergence generally reflects the signature

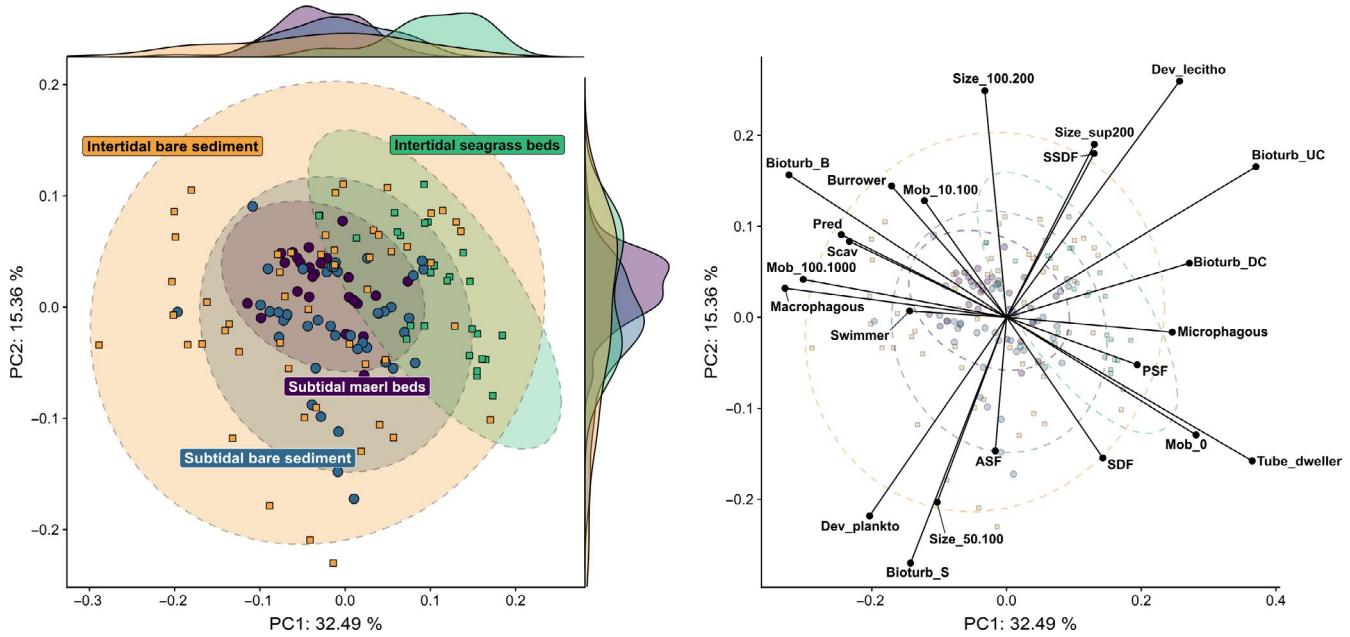

FIGURE 5 Principal component analysis (PCA) of Hellinger-transformed trait modality abundances. Left panel: Samples are displayed in scaling 1 in the central panel. The shapes of the points reflect differences in the tidal levels and sampling methods: squares represent intertidal habitats sampled using sediment cores and circles represent subtidal habitats sampled using Smith-McIntyre grabs (see Figure 1). The densities of points for each habitat along the first and second axis are displayed in the corresponding margins. Within-habitat variability is comprised of both spatial and temporal variations (see Figures 1 and S1). The first two principal component analysis axes represented account together for 47.85% of the total variance of Hellinger-transformed trait composition. Right panel: modalities whose variances along these two axes represent more than 30% of their total variances (assessed with the function goodness; vegan). For abbreviations, please refer to Table 1

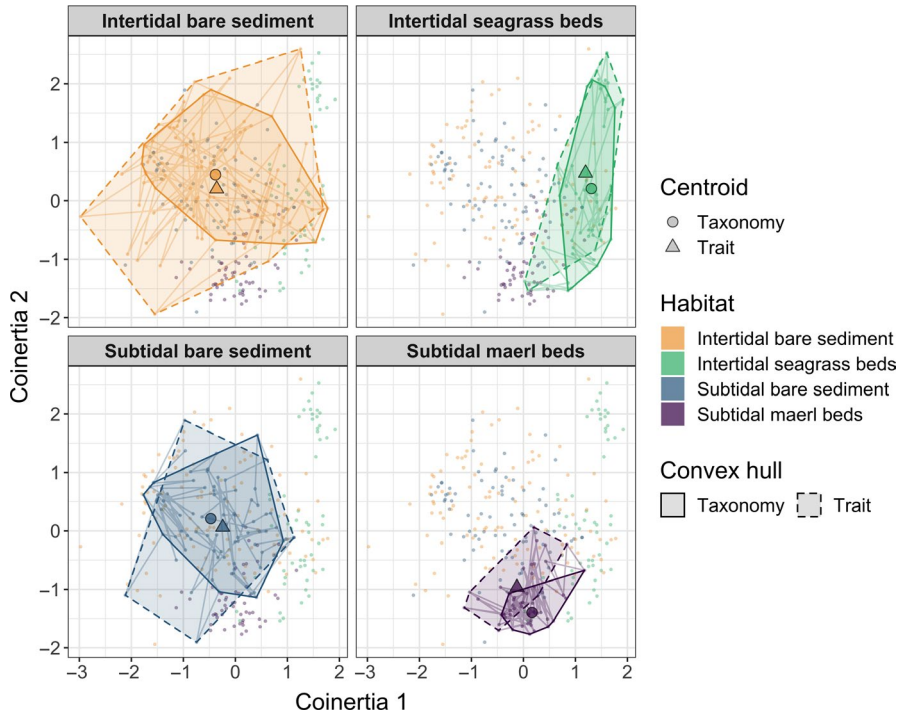

FIGURE 6 Coinertia analysis between the taxonomic β diversity patterns represented in Figure 2 and the trait-based patterns of Figure 5. Five axes of each ordination were kept for the coinertia analysis; the RV coefficient between the two ordinations was 0.62. The four panels highlight the two-dimensional convex hull covered in the coinertia ordination by the assemblages of each habitat in terms of taxonomy (plain border) and trait composition (dashed border). All four panels are based on a single coinertia analysis involving all samples, represented in the background of each panel with colours corresponding to the four habitats. The centroid positions of the assemblages of each habitat in terms of trait and species composition are represented by distinctive symbols. Lines link the two points representing a sample in the species and trait spaces, respectively

of environmental filters (Perronne et al., 2017) as observed in some intertidal bare sediment (IBS) bearing harsh conditions that require unique adaptations for species to establish and persist (Defeo & McLachlan, 2005). Alternatively, trait divergence is expected to arise from strong competitive interactions (Perronne et al., 2017). These are thought to be rather weak in soft-bottom environments although they may be fairly intense in sheltered conditions and among closely related species such as the polychaetes on which focuses this study (Defeo & McLachlan, 2005; Wilson, 1990). In the intertidal, however, over-dispersion was only observed in the IBS with the lowest richnesses and abundances. Such small assemblages with high niche specialization and functional evenness evoke initial successional stages (Song & Saavedra, 2018) that may result from the strong disturbance regimes of intertidal environments, which constantly reset communities (Defeo & McLachlan, 2005). Therefore, SES variability in IBS is likely to reflect different "ecological ages" of assemblages (Bracewell, Johnston, & Clark, 2017), rather than different assembly mechanisms, abiotic constraints largely governing these IBS communities (Quillien, Nordström, Guyonnet, et al., 2015).

Standard Effect Size values were more stable in biogenic habitats, reflecting less variation in the degree of environmental severity than in bare sediment. A first potential explanation for this difference is that biogenic habitats would themselves be found in a more restricted set of environmental conditions that bare sediment. However, the sites monitored were here chosen to encompass a spectrum as broad as possible of the environmental conditions found in the region (e.g., see for seagrass meadows Boyé et al., 2017). In agreement, the granulometry observed within bare and biogenic habitats suggests that, although the range of environmental conditions encompassed within each habitat slightly differs, this factor alone cannot explain the greater stability found in biogenic habitats (Figure S2). This stability may be partly attributed to the role of refugia from abiotic constraints that these biogenic habitats may play (Bulleri et al., 2018). The latter is supported by the absence of strong trait convergence within these habitats. In particular, MB assemblages consistently exhibited trait over-dispersion, which indicates the presence across environmental gradients of niche differentiation promoting mechanisms among species (Perronne et al., 2017). MB structure may promote niche partitioning by dampening the effects of environmental constraints, thereby enhancing the strength of biotic interactions, as well as by providing a higher fine-scale heterogeneity than bare sediment (D'Andrea & Ostling, 2016). Indeed, MB provides foundation for the establishment of a whole range of epiphytes (Peña, Bárbara, Grall, Maggs, & Hall-Spencer, 2014), which creates a great diversity of living spaces for polychaetes through a hierarchy of facilitative interactions called "habitat cascade" (Thomsen et al.,

2010). This process results in high heterogeneity at fine scale (Figure 1e) and is associated with great niche diversity (Grall, Le Loc'h, Guyonnet, & Riera, 2006).

A different functional signature was observed for seagrass beds (SB). In line with observations made on the whole infaunal diversity of Baltic *Zostera marina* meadows (Henseler et al., 2019), our trait-based approach on polychaetes revealed that SB high local richness was linked to abundances concentrated in specific trait combinations. Resource-rich environments may favour a small number of optimal suites of traits when competition is focused around a few limiting resources (Perronne et al., 2017). Such competitive dominance may occur in SB: the substantial amount of detrital material fuelling seagrass food webs (Ouisse, Riera, Migné, Leroux, & Davoult, 2012) may act as a core resource (Ricklefs, 2012) leading to the observed dominance of sessile microphagous suspensive and deposit feeders. Contrary to expectations (Perronne et al., 2017), however, competitive dominance did not translate into functional convergence in these SB, trait dispersion matching random expectations. This result, and the substantial contribution of rare species with rare traits, suggests an important presence of transient species with a large stochastic component (Umaña et al., 2017). Seagrass patches mitigate low tide exposure and provide refugia of lower hydrodynamic intensity, which constitute sink areas for larvae and organisms in highly hydrodynamic settings such as intertidal environments (Boström & Bonsdorff, 2000; Bouma, Olenin, Reise, & Ysebaert, 2009). This may lay foundations for mass effects, allowing the persistence of numerous rare, likely maladapted, species dispersing from neighbouring habitats (Hillebrand, Bennett, & Cadotte, 2008). Such source–sink dynamics are supported by the dynamic equilibrium observed on the whole communities of these SB with high species replacement in space and time accompanied by highly stable species richness (Boyé et al., 2017). Similar β diversity patterns have been reported in other intertidal meadows (Barnes, 2013), which suggests that this large stochastic component of SB diversity is not limited to those under study. We therefore propose a mechanism involving a mix of competitive dominance and mass effect encompassing the different effects of seagrass engineering process (Bouma et al., 2009), which would explain the preservation of similar functional structure and dominant functional entities across geographically distant intertidal seagrass meadows despite high stochasticity (Barnes & Hendy, 2015).

TABLE 3 Recommended actions at regional scale based on our results, as a function of the conservation targets

Conservation targets	Proposed actions based on our results
Preserving current taxonomic diversity	Preserve biogenic habitats across the region, ideally through protection of several maerl and seagrass beds encompassing contrasted environments.
Preserving current functional diversity	Preserve any single maerl bed, a few beds selected for their complementarity may protect most of the regional diversity.
	Preserve seagrass-associated β diversity at the regional scale.
	Preserve bare sediment β diversity at the regional scale, including their temporal asynchrony in intertidal environments.
Ensuring the maintenance of functional diversity on the long-term	Preserve maerl beds and their β diversity all over the region.
	Protect landscapes in which intertidal seagrass beds are embedded.

4.2 | Scaling-up to guide conservation at regional scale through functional β diversity

According to coinertia analyses and RV coefficients, changes in taxonomic composition across sites and years were strongly associated to changes in trait composition in SB and subtidal bare sediment (SBS) while they were not in IBS and MB. In IBS, functional changes were exacerbated when compared to taxonomic changes, suggesting strong functional specialization of communities in space and time. Overall, the high taxonomic β diversity observed in bare habitats lead to a functional complementarity of communities at broad scale (Bond & Chase, 2002). Indeed, the functional volume occupied by species appeared similar for bare sediment and biogenic habitats at regional scale despite lower local functional richness in bare sediment, the latter being compensated by higher functional β diversity. Such functional complementarity may enhance the functioning of ecosystems because different species best perform different functions in different environments (Hautier et al., 2017). While conservation policies largely focus on local community diversity and their taxonomic complementarity (Bush, Harwood, Hoskins, Mokany, & Ferrier, 2016), we emphasize the need to also consider their functional complementarity and the multiple facets of β diversity (Mori et al., 2018). For example, the functional consequences of the homogenizing effects of eutrophication on intertidal bare sediment assemblages (Quillien, Nordström, Gauthier, et al., 2015; Quillien, Nordström, Schaal, Bonsdorff, & Grall, 2016) may be as large as the loss of seagrass-associated infauna based on our estimates on polychaetes.

Preserving β diversity is also critical to ensure the stability and maintenance of ecosystem functioning in the face of changing environments as β diversity allows different species to become increasingly dominant when and where they perform best (Isbell et al., 2018; Wang & Loreau, 2014). In this perspective, our results suggest that maintenance of biogenic habitats is essential to ensure the long-term maintenance of benthic ecosystem functioning. Maerl-associated assemblages were characterized by distinct taxonomic composition at regional scale compared to the other habitats. However, coinertia showed that these taxonomic differences were not traduced by as much differences in terms of trait composition. This suggests that, despite taxonomic differences, there is a degree of functional redundancy between maerl assemblages and those of other habitats. Additionally, MB assemblages central positions in the trait-based PCA and their average 30%

occupancy of the regional trait space suggest that irrespective of taxonomic composition, their high richness ensures that many of the functional entities of the region are found within each MB assemblage and that across different environments. Therefore, MB assemblages may serve as sources of species over the whole region to replenish any of the functional entities that may be lost in subtidal sediments. Hence, their high taxonomic and functional richness is not an argument in favour of the selective protection of a few beds to preserve the whole diversity of subtidal soft bottoms; it is on the contrary a strong case in favour of the protection of multiple maerl beds across the region in order to maintain a spatial and temporal insurance for benthic ecosystem functioning (Isbell et al., 2018).

However, not all highly diverse systems are associated with high functional redundancy (Mouillot, Bellwood, et al., 2013; Mouillot et al., 2014) depending on the linkages between species functional rarity and rarity in terms of abundances and occurrences (Violle et al., 2017). As highlighted here in the differences between MB and SB, the relative contribution of dominant and rare species to functional redundancy may vary among benthic environments (Ellingsen, Hewitt, & Thrush, 2007; Mouillot, Bellwood, et al., 2013). SB promote species with specific trait combinations, which provides stability and redundancy for the functions associated with the promoted species. For instance, the consistent upward and downward conveying activities of the microphagous species favoured through competitive dominance may contribute to the stability of sedimentary processes within SB (Bernard et al., 2014). However, variation of SB assemblages led, as in bare sediment, to differences in functional composition because transient species with rare traits make up most of their functional richness. Therefore, SB high taxonomic diversity is associated with redundancy of a few functions only, meaning that SB functional diversity remains highly vulnerable to species loss (Mouillot et al., 2014). In addition, while rare species may have a substantial role in the performance of ecosystems (Soliveres et al., 2016), it remains unclear to what extent transient species are directly involved in ecosystem functioning in the case of SB (Umaña et al., 2017). Nonetheless, transient species are critical in providing insurance for the functioning of benthic habitats (Hewitt, Thrush, & Ellingsen, 2016). While dominant species often govern the short-term resilience of ecosystems, rare species could determine their long-term dynamics (Arnoldi, Bideault, Loreau, & Haegeman, 2018). Because their presences depend on mass effect, ensuring the long-term functioning of SB requires not only maintenance of the meadows themselves, but also of the heterogeneity of the seascape in which they are embedded, which has also been highlighted as a key requirement to maintain seagrass nursery functions (Olson, Hessing-Lewis, Haggarty, & Juanes, 2019).

Importantly, by focusing solely on polychaetes, we only accounted for some of the indirect effects of foundation species on ecosystem functioning. However, they also have other direct and indirect effects (Alsterberg et al., 2017; Liu et al., 2018) so that their contributions extend beyond those highlighted here, which should be viewed as conservative estimates. Furthermore, it should be acknowledged that other taxonomic groups might respond differently than polychaetes (Dauvin, Andrade, De-la-Ossa-Carretero, Del-Pilar-Ruso, & Riera, 2016). However, polychaetes often represent an important fraction of benthic community diversity, abundance and biomass (Hutchings, 1998) and the wide diversity of their ecological strategies (Jumars et al., 2015) make them particularly interesting indicators of the state of benthic ecosystems (Giangrande, Licciano, & Musco, 2005). Therefore, we consider that our results could reasonably be scaled-up to the overall diversity inhabiting benthic sediment, which is supported by the similarities between the present results and those reported by Henseler et al. (2019) for the whole infauna of seagrass meadows.

5 | CONCLUSIONS

Overall, biogenic habitats emerged as a major factor governing the structure and composition of polychaete assemblages at the regional scale, consistently promoting their α diversity across disparate environments. These results confirm patterns previously reported worldwide and reaffirm the conservation value of seagrass and maerl beds (Hemminga & Duarte, 2000; Riosmena-Rodríguez et al., 2017). Our results suggest that biogenic habitat provide spatial and temporal insurance to the functioning of benthic ecosystems, which is absent in bare sediment, so that preserving the integrity of foundation populations appears as a key priority to mitigate biodiversity loss on the long-term (Bulleri et al., 2018). However, we show that different mechanisms underlie their diversity, leading to different vulnerabilities of their associated assemblages that should be taken into account in conservation plans to appropriately predict and manage the functional consequences of future biodiversity changes. Although locally poorer, bare sediment assemblages have similar contributions to the functional richness of the region because of their high spatial and temporal β diversity. As such, significant threats to the functioning of benthic ecosystems may also emerge at broad scale from their homogenization. In light of these results, and given the substantial loss already experienced by biogenic habitats (Airoldi & Beck, 2007), important efforts should also be devoted to the understanding and conservation of bare sediment β diversity.

While conservation policies largely focus on local community diversity and their taxonomic complementarity (Socolar et al., 2016), our study reinforces the need to better consider their functional complementarity (Mori et al., 2018). The decoupling we described between taxonomic and functional β diversity is increasingly recognized (Devictor et al., 2010; Loiseau et al., 2016) and was previously reported for bare soft sediment (Bremner, Rogers, & Frid, 2003), meaning that functional priorities may not always match conservation priorities stemming from other biodiversity facets. Here, we suggest that the relationship between

these two biodiversity facets may also depend on the habitat and the presence of foundation species. This supports the need to directly incorporate functional aspects in the design of conservation schemes to implement a multi-faceted conservation of biodiversity (Pollock, Thuiller, & Jetz, 2017), capable of promoting ecosystems resilience in the face of current environmental changes (Thrush & Dayton, 2010). In this respect, our results fill important gaps in the understanding of benthic functional α and β diversities at broad scale (Airoldi et al., 2008) and thereby, provide key guiding elements for preserving the integrity of seafloor functioning (see Table 3). The broad-scale monitoring data used in this study allowed us to bridge knowledge of communities across scales, linking the mechanisms governing diversity at local scales to the vulnerability of ecosystems at regional scale. This further highlights the key role of such monitoring programmes that allow ecologists to bring the conclusions of theoretical and fine-scale experimental studies closer to the spatial and temporal scales at which biodiversity is lost and at which society manages and benefits from nature (Isbell et al., 2017).

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DATA AVAILABILITY STATEMENT

All data from the REBENT monitoring programme (http://www.rebent.org) are available in the Quadrige database (http://envlit.ifremer.fr/resultats/base_de_donnees_quadrige) and in the database of the marine observatory of the IUEM (available upon request: https://www-iuem.univ-brest.fr/observatoire).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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