Title: Leaf size doesn't matter: environment shapes eelgrass biodiversity more than a foundation species' traits.

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Abstract

Aim: Understand the ecological processes that shape community composition in eelgrass meadows along the coast of France at local and regional scales.

Location: Northeastern Atlantic.

Methods: Combining taxonomic and trait-based approaches with structural equation modeling, we explored the mechanisms governing community assembly in five meadows located over a distance of 800 km along the French coast in the Northeast Atlantic. We assessed the spatial variability of eelgrass-associated invertebrate communities as affected by environmental parameters or morphological traits of the eelgrass and linked these mechanisms to their impacts at local and regional scales through analyses of the taxonomic and functional α and β diversities. We then quantified the direct and indirect effects of environmental factors on macrofaunal structure and composition.

Results: Eelgrass meadows locally favored higher species abundance, diversity, and functional traits present in the community relative to nearby bare sediments. At the regional scale, eelgrass diversity was comparable between sites, with high species turnover observed among them, and each site being characterized by different species and different sets of traits. These differences were due in part to morphological traits of the meadows, but the explanatory variables that best explained the differences among the meadows were environmental conditions, including temperature, current velocity, and Δ water level.

Main conclusions: Meadows appear to harbor subsets of species from the regional species pool, rather than harboring eelgrass-specific assemblages. The processes that maintain seagrass diversity appear to reflect a seascape-scale meta-community composed of many habitats connected by source-sink dynamics. Given that eelgrass enhances the diversity and abundance of species found in neighboring habitats, conservation programs should consider ecosystem-level protection spanning multiple habitats, including eelgrass, in order to maximize the protection of biodiversity.

KEYWORDS

Beta diversity, edge effect, engineering species, functional diversity, structural equation modeling, *Zostera marina*

INTRODUCTION

Marine biodiversity contributes to healthy and resilient ecosystems, but is currently under threat by a multitude of human activities such as climate change, overharvesting and pollution (Isbell et al., 2017). In order to make informed decisions about seascape (Kavanaugh, 2019) management and conservation, it is essential to understand the processes that control the distribution of diversity across marine habitats. Biodiversity varies in response to processes taking place at both local and regional scales (Boström et al., 2006; Leibold et al., 2004; Underwood & Chapman, 1996). Therefore, understanding community assembly requires multiple scales of observations (Chase et al., 2018; Whippo et al., 2018). At broad geographic scales, evolutionary, geological and colonization histories define a regional species pool, referred to as γ-diversity (Mittelbach & Schemske, 2015; Whittaker, 1960, 1972). At finer scales, biotic interactions (predation, competition) and abiotic conditions within habitats filter species from the regional pool leading to what is known as α-diversity (Crist & Veech, 2006; De Troch et al., 2001; Sanders et al., 2007; Thompson et al., 2020; Whittaker, 1960, 1972). Interactions between local and regional processes generate spatial gradients in community structure known as β-diversity (Airoldi et al., 2008; Anderson et al., 2011; Thompson et al., 2020; Whittaker, 1960, 1972). Examining each of these components of diversity is essential for determining which factors most influence communities of a given habitat type.

It is now widely recognized that the integration of functional information based on species traits provides a complementary understanding of community functioning along spatial scales (Díaz & Cabido, 2001; Pavoine & Bonsall, 2011; Stegen & Hurlbert, 2011; Swenson et al., 2011). Indeed, comparing taxonomic and functional diversity can provide insights into the ecological processes that shape community composition (Mori et al., 2018; Swenson, 2011; Villéger et al., 2010) and the impact of biodiversity loss on ecosystem functioning (Burley et al., 2016; Cadotte et al., 2011). For example, trait homogenization within communities, when only species with a specific set of traits are found under certain conditions, are indicative that selective processes are at work, such as environmental filtering (Münkemüller et al., 2020; Perronne et al., 2017). Comparing taxonomic and functional diversity (on the basis of presence–absence and abundance data) can therefore provide key insights into the mechanisms affecting biodiversity.

Differences in biodiversity among assemblages (β-diversity) can also be considered as two separate components: species turnover (the replacement of species or functional strategies in one assemblage compared to another) and nestedness (differences in richness when one assemblage is a subset of another, (Baselga, 2010, 2012; Legendre, 2014; Villéger et al., 2013). Quantifying the relative contributions of turnover and nestedness to β-diversity can improve our understanding of the ecological processes that structure communities. Indeed, two communities may have high taxonomic or functional β-diversity as a result of different processes that can be disentangled by partitioning the variation into turnover and nestedness. For example, high β-diversity may be due to high functional turnover, indicating niche differentiation between communities (Loiseau et al., 2017; Villéger et al., 2013), while high β-diversity could also result from high nestedness (accompanied then by low functional turnover), if the species hosted by one community represent only a small subset of the functional strategies present in the other community, indicating a different niche filtering intensity (Loiseau et al., 2017; Villéger et al., 2013). It is therefore important to consider the contributions of both turnover and nestedness in comparisons among communities.

Biodiversity is typically greater in structurally complex compared to homogeneous habitats (Lapointe & Bourget, 1999; MacArthur & MacArthur, 1961). Many communities coexist in habitats that have been modified by organisms that have critical effects on habitat structure and ecosystem functions; these are called foundation species (Dayton 1972). Foundation species not only complexify the habitat but also control the availability of resources for other organisms (Ellison, 2019; Sarà, 1986). By modifying habitat, foundation species can influence community assembly and its long-term persistence through numerous mechanisms such as niche partitioning (Willis et al., 2005), altering competitive and predator-prey interactions (Costello et al., 2015), or providing refuge from physical stressors (Bulleri et al., 2016; Jurgens & Gaylord, 2018; Scheffers et al., 2014). Habitat complexity also favors microhabitat heterogeneity (Bulleri et al., 2016; Lassau et al., 2005; Schöb et al., 2012; Williams et al., 2002), which may attract or deter certain species thereby influencing local diversity (Swenson & Weiser, 2010; Walters & Wethey, 1991; Wood et al., 2015). Because community composition can vary greatly within habitats across environmental gradients (Boström et al., 2006; Boyé et al., 2017), studying the effect of habitat structural complexity on the associated communities improves our understanding of the processes structuring biodiversity over various geographic scales (Airoldi et al., 2008). Foundation species are also likely to mediate the impact of climate and anthropogenic change on biodiversity, particularly because they tend to buffer or attenuate change (Bulleri et al., 2018; Sunday et al., 2017). While foundation species exert many direct effects on the communities they support, less is known about the indirect effects that they or the environment may exert on communities. For many foundation species, a comprehensive understanding of the direct and indirect influences on biodiversity are lacking (Miller et al., 2018), which limits our ability to in turn predict the cascading effects of anthropogenic and climate change on associated fauna.

Zostera marina (Linnaeus, 1753) is a flowering marine plant that occurs from temperate to subarctic regions (Short & Frederick, 2004), forming meadows that are recognized as being among the most important coastal marine ecosystems on the planet (Costanza et al., 1997; Dewsbury et al., 2016; Duarte et al., 2008; Duffy, 2006a). Eelgrass is a foundation species, providing essential functions and services including coastal protection, erosion control, nutrient cycling, water purification, carbon sequestration, as well as food and habitat for a variety of species (Barbier et al., 2011; Cullen-Unsworth & Unsworth, 2013; Duarte, 2002; Fourqurean et al., 2012; Healey & Hovel, 2004; K. L. Heck et al., 2003; Orth et al., 2006; Schmidt et al., 2011). Eelgrass can have a strong influence on the spatial distribution of associated fauna by altering the hydrodynamics of the marine environment (Fonseca & Fisher, 1986), providing abundant resources, available surface area, and increased ecological niches. Meadows also provide protection from predation by providing greater habitat complexity both above and below-ground (Gartner et al., 2013; Kenneth L. Heck & Wetstone, 1977; Orth et al., 1984; Reynolds et al., 2018). At the local scale, it is generally accepted that meadow complexity parameters (e.g. biomass, shoot density, leaf length) directly influence species-level responses (e.g. growth, mortality, predation, movement, reproduction). The variability of eelgrass structure in relation to its physical environment is fairly well understood (Boyé et al., 2022; Fonseca & Bell, 1998; Frederiksen et al., 2004; Robbins & Bell, 2000), as is the effect of the environment on the community structure (Blake & Duffy, 2012; Douglass et al., 2010; Yeager et al., 2019). However understanding how these components interact, and the relative importance of different environmental and biotic factors in explaining biodiversity at multiple spatial scales has proven more difficult (Bowden et al., 2001; Hovel et al., 2002; Turner et al., 1999). Indeed most of the potential cascading effects studied to date involve the loss or replacement of foundation species (Airoldi et al., 2008; Ellison et al., 2005; Pessarrodona et al., 2019; Sorte et al., 2017). Understanding how the environment affects biodiversity directly or indirectly by modifying traits of the foundation species, may help us better understand how eelgrass or other foundation species may mediate the effect of climate change on coastal biodiversity (Bulleri et al., 2018; Sunday et al., 2017).

In this study, the taxonomic and functional diversity of assemblages associated with five *Z. marina* meadows occurring over a distance of 800 km along the coast of France were investigated with the objective of determining which factors control community composition within this habitat. To this end, we examined **α**- and **β**-diversity of species- and trait-based descriptors, focused on polychaetes, gastropods and bivalves; three diverse groups exhibiting a wide range of ecological strategies (Jumars et al., 2015) and having central roles in ecosystem functioning through activities such as bioturbation or trophic regime (Duffy et al., 2015; Queirós et al., 2013). Specifically, we asked the following questions: (i) Are there differences in terms of abundance, species and trait diversity at fine spatial scales within eelgrass meadows? We tested the hypotheses that structurally complex habitats (meadows) host higher diversity than homogeneous habitats (bare sediment) and that stable habitats (meadow cores) host greater diversity than unstable habitats (meadow edges). (ii) Are there differences in the taxonomic and functional diversity of assemblages from different geographical sites? If so, what are the underlying processes that explain differences in diversity among meadows? We tested the hypothesis that the five meadows would have similar levels of species and functional **α**-diversity, but that species composition would change from meadow to meadow based on the effect of environmental variables on the regional species pool (i.e., **β**-diversity would vary). (iii) Finally, what are the direct and indirect effects of environmental factors on assemblage structure? Can we quantify and account for indirect or cascading effects that affect community structure, using piecewise structural equation modeling (Lefcheck et al., 2015)? We tested the hypothesis that the environment and characteristics of the foundation species affect community structure at different scales and to different degrees. By addressing these questions, we aim to improve our understanding of community assembly rules at work in *Z. marina* meadows, which will ultimately help guide conservation measures in this important habitat.

METHODS

Study area and sampling methods

Five sites along the coast of France were selected to quantify diversity in benthic macrofaunal assemblages associated with *Z. marina* meadows: three in the English Channel, and two in the Bay of Biscay (**Fig. 1**). These sites were chosen to cover a range of environmental conditions in which *Z. marina* meadows can be found: from exposed, fully marine conditions (Ile d’Yeu and Chausey), to semi-open habitats (Dinard and Sainte-Marguerite; Hily et al., 2003, Boyé et al., 2017), to sheltered bays with turbid waters (Arcachon). Sampling was carried out in autumn 2019 (late September to mid-November) following a standardized protocol at each site. This sampling period corresponded to the season of maximum canopy development for eelgrass and to the post-recruitment period for most macroinvertebrate species (Grall, 2002; Moore & Short, 2006). To study community diversity and species composition associated with *Z. marina* meadows over short spatial scales, benthic macrofauna were sampled in three different modalities at each sampling site. These modalities were established using cartography of meadows at different time points and/or aerial photography of the meadows, which allowed to identify a "core" modality characterized by perennial areas colonized by *Z. marina*, an "edge" modality characterized by recently colonized and temporally unstable eelgrass areas, and a "bare sediment" modality not colonized by *Z. marina* (**Fig. 1, Fig S1**). Typically, core areas have been occupied by eelgrass over the past 10 years or more (up to 80 years for Chausey) whereas edge areas were colonized more recently (last few years). The only exception to this was Ile d’Yeu where the meadow had not previously been mapped, so that core and edge quadrats were assigned based on their spatial position relative to the extent of the meadow and local expert knowledge.

In each site, two quadrats measuring 30 by 25 meters were deployed for each modality (*i.e.* core, edge and bare sediment), and were at least 10 m apart. In each quadrat, three samples were randomly collected by pooling the eelgrass shoots and sediment retrieved with three 0.03 m^2 manual push cores and placed into 1 mm nylon mesh collection bags, which allowed pre-sieving and washing away most sediments directly in the field (**Fig. 1**). Once in the laboratory, the content of each sample was preserved in 70% ethanol. To ensure optimal species fixation, ethanol was replaced every 2 days, for a total of three renewals. In the laboratory, cores were sieved on a 1 mm mesh. Macrofauna was then extracted from the sediments and counted. All individuals belonging to polychaetes, gastropods and bivalves were identified to the lowest taxonomic level possible, most often to the species level. All species names were used according to the World Register of Marine Species and references used for taxonomic identification are listed in **Appendix S1** in Supporting Information. To ensure consistent taxonomic resolution across samples, a unique operator (A. Muller) was involved and uncertain identifications were cross-checked by a taxonomic expert (G. Droual).

Morphological and structural trait measurements

All shoots in each sample were counted to measure *Z. marina* densities. Five shoots were randomly selected for morphometric measurements, which included sheath height, leaf length and width, and the number of leaves per shoot. Sheath height was measured from the first node to the leaf separation mark. The length of each leaf was measured from the node mark to the apex. The width was taken at mid-length. The biomass of leaves, sheaths, roots and rhizomes were measured separately for each of the 2 core and 2 edge quadrats (i.e. a total of 15 measurements in each quadrats) in each of the 5 sites, and were measured as dry weight following 48 hours of desiccation at 60°C. Total biomass and densities were expressed per square meter. To assess the relative investment of *Z. marina* between its above-ground and below-ground compartments, we calculated the ratio between the biomass of leaves and sheaths and the biomass of roots and rhizomes (Boyé et al., 2022). Average leaf, root and rhizome biomass per shoot were estimated by dividing the total biomass by the shoot densities. The Leaf Area Index (LAI) was then calculated as the ratio between the total leaf area of the plant and the substrate area it covers. For all other variables (densities, sheath height, leaf length and width, number of leaves per shoot, proportion of broken leaves), mean values (and standard errors) were calculated. Broken leaves were retained in the calculation of average leaf length to reflect the physiological and mechanical impacts of the eelgrass environment (Boyé et al., 2022). However, leaves cleanly cut by the corer were removed to avoid bias related to the sampling method. All morphological and structural trait measurements are listed in **Tab. S1.2**.

Environmental variables

Two sediment cores were collected from each quadrat for measuring grain size distribution and organic matter content, respectively (**Fig. 1**). Sediments were dried in an oven (72 h at 60°C), separated into 25 fractions for which the weights were measured. Fractions were afterwards grouped into gravels (> 2 mm), sand (63 µm to 2 mm) and silt and clay (< 63 µm; Fournier et al., 2012). Loss-on-ignition (450°C for 4 h) estimates of organic matter in sediments was conducted.

Information regarding physical environmental conditions at each site (e.g., water temperatures, salinities and current velocities) were obtained from the publicly available MARC database (https://marc.ifremer.fr/en) which modeled physical oceanographic parameters using the MARS3D hydrodynamic model (2.5 km resolution, 40 depth levels; https://marc.ifremer.fr/en). All variables were extracted daily for the year prior to the study at midday near the sediment surface. Biogeochemical environmental variables were retrieved from the ECO-MARS3D model also available from the MARC database (4 km resolution, 30 depth levels; https://marc.ifremer.fr/en). The biogeochemical variables included suspended inorganic particulate matter, ammonium, nitrate, phosphate and dissolved oxygen. Given that the English Channel and Bay of Biscay have different tidal regimes, from mega-tidal in the central English Channel to meso-tidal in the southern Bay of Biscay, the amplitude of water level over a meadow varied depending on the geographical location of the sites. The estimated average changes in water level (Δ water level) over the meadows were obtained based on the difference between the maximum and minimum water level predictions for each site based on the harmonic components of tidal heights and currents computed from the MARS3D models (https://marc.ifremer.fr/en; Le Roy and Simon, 2003) and the TidalToolBox (Allain, 2016). All environmental variables are listed in **Tab. S1.2**.

Biological traits

To assess functional diversity, biological traits were scored for polychaetes, gastropods and bivalves, three phylogenetically diverse groups composed of a large diversity of species exhibiting a wide range of ecological strategies (Aldea et al., 2008; Gosling, 2015; Jumars et al., 2015; Lassau et al., 2005; Teso et al., 2019). Eight biological traits (divided into 30 modalities) were selected (**Tab. S2.2**), providing information related to the ecological functions performed by the associated macrofauna. These traits characterized the maximum size, feeding and reproductive ecology, mobility, and bioturbation potential of the species (**Tab. S2.2**) and were chosen to reflect key biological and ecological processes (Queirós et al., 2013; Solan et al., 2004; Thrush et al., 2006). Species were scored for each trait modality based on their affinity using a fuzzy coding approach (Chevene et al., 1994), where multiple modalities can be assigned to a species if appropriate, and allowed for incorporation of intraspecific variability in trait expression. A trait matrix containing total abundances of each modality by sites was calculated using the matrix product of the site-species matrix with the species-trait matrix, after normalizing scores to 1 per trait and species. Information for polychaetes was primarily extracted from Fauchald et al (1979), Jumars et al (2015), and Boyé et al (2019). Information for gastropods and bivalves was obtained either from biological trait databases (www.marlin.ac.uk/biotic, www.univie.ac.at/arctictraits) or from publications (e.g. Bacouillard, 2019; Martini et al., 2020; Queirós et al., 2013; Thrush et al., 2006). Information was collected at the lowest possible taxonomic level and when missing was based on data available in other species of the genus, or in some cases, in the same family (only for traits with low variability for these families).

Statistical analyses

We studied changes in total abundance, taxonomic and functional diversity across different spatial scales, from within habitat modalities (edge *vs.* core) to local habitat conditions (meadow *vs.* bare sediment) to regional habitat conditions (meadow *vs.* meadows) using three different characterizing α-diversity measures. Taxonomic diversity was estimated using the Simpson index for each modality in each site to characterize the α-diversity of polychaetes, gastropods and bivalves and its spatial variation. The Simpson diversity index was chosen because of its property of reducing the influence of rare species (Hill, 1973), to emphasize the effect of species accounting for most of the total abundance. The functional structure of polychaetes, gastropods and bivalves assemblages was characterized using two complementary indices: functional richness (FRic) and functional evenness (FEve, Laliberte & Legendre, 2010; Mouchet et al., 2010; Villéger et al., 2008). Differences between core vs edge and meadow vs bar sediment were tested with two-way nested ANOVA and meadow vs meadow were tested with one-way ANOVA. Pairwise comparisons were carried out with the Tukey-test ($p < 0.05$).

Community structure associated with *Z. marina* among the five sites were compared using Principal Component Analysis (PCA) of Hellinger-transformed species abundances for polychaetes, gastropods and bivalves combined. Abundance based dissimilarities can be strongly influenced by overabundant species or by a high proportion of rare species. Applying a Hellinger transformation to abundance data allows Euclidean-based methods to be used, while also not overweighting rare species (Legendre & Gallagher, 2001). In addition, Sørensen's dissimilarity index (Sørensen, 1948) was calculated based on presence-absence data for each community sample. For each pair of samples, taxonomic β-diversity and its two components, turnover and nestedness, were computed using the Baselga partitioning scheme (Baselga, 2017; Schmera et al., 2020). Functional β-diversity was computed based on fuzzy correspondence analysis, where axes were synthetic components summarizing functional traits (Mouillot et al., 2014; Villéger et al., 2011). The first two axes were used for calculating the Jaccard’s dissimilarity index according to Villeger’s equation (2013) for all pairwise comparisons between samples (1) belonging to the same site (within site), or (2) belonging to different sites (among site).

A Redundancy analysis (RDA) was used to investigate to which extent species composition was affected by two sets of predictors, namely on site environmental variables and morphological and structural characteristics of *Z. marina*. Collinear variables were removed using variance inflation factors (VIF) with a threshold of five as recommended in Legendre & Legendre (2012), which resulted in the removal of some of the variables characterizing the distribution of the sediment, salinity, dissolved oxygen and nutrients. Then, a stepwise selection based on adjusted coefficients (R^2_{adj}) was applied to remaining environmental variables and the morphological characteristics of *Z. marina* (Blanchet et al., 2008). The results of the RDA were used to ultimately select six environmental and four morphometric variables that most explained the variation in the community dataset (**Fig. S5.2**) - which included: temperature, current velocity, Δ water level, mean grain size, mud content, below-ground biomass, leaf width and leaf length. These variables were then used to construct piecewise structural equation models (SEM, Lefcheck, 2016) to explore the direct and indirect effects (through eelgrass trait responses) of environmental factors on the structure and composition of the macrofauna. This technique allows fitting complex networks, facilitating the identification of cascading effects (Airoldi et al., 2008; Barnes, 2017; Elbrecht et al., 2017; Ellison et al., 2005; Lefcheck et al., 2015; Pessarrodona et al., 2019; Wernberg et al., 2012). We implemented a model that considered the effects of environmental and morphometric variables on regional gradients of taxonomic composition (using the first two axes of the PCA on Hellinger-transformed abundances), and on local diversity indices (using total abundance, species richness, FRic, and FEve).

All diversity and functional metrics calculations and statistical analyses were performed using the G2Sd (Fournier et al., 2014), 'ade4' (Dray & Dufour, 2007), 'vegan' (Oksanen et al., 2019), 'FD' (Laliberté et al., 2014), 'betapart' (Baselga, 2012) packages and multivariate analysis in the form of piecewise SEM was conducted using the packages 'nlme', and 'piecewiseSEM' (Lefcheck et al., 2015) in R 4.0.3 (R Development Core Team, 2008).

Results

A total of 90 community samples were collected in the five sites, for a total of 9277 individuals and 138 species (56 molluscs and 82 polychaetes). Rare species accounted for a large proportion of the samples: 43% of the species were observed in a single sample and 38% were represented by one or two individuals.

Spatial patterns of α diversity

The abundance and diversity of polychaetes, gastropods and bivalves differed among core, edge and bare sediment modalities (**Tab. 1, Fig. S1.2**). Samples collected within the meadows (core + edge) showed marked differences in community structure compared to bare sediments: the mean abundance (ind.m^{-2}) and the average number of species was significantly higher in meadows than in bare sediments at all localities, except Ile d'Yeu where abundances in meadows and bare sediment were not significantly different (**Tab. 1**). Communities associated with meadows showed greater variation in both mean abundance (2384 to 6188 ind.m^{-2}) and average number of species (11 to 19), than the more homogeneous bare sediments (Ile d'Yeu excluded) which had a abundances of only 303 to 2729 ind.m^{-2} and 4 to 11 species (**Tab. 1**). Similarly when looking at functional diversity indices, bare sediments had small, trait-poor functional space (low FRic) with evenly distributed abundances (high FEve). In comparison, meadows had larger functional spaces (higher FRic) with abundances being concentrated on a few traits (low FEve). This indicates that the dominant species shared the same functional traits and that a large part of the functional space was occupied by less abundant species with rarer traits.

In contrast to mean species richness and Simpson index, which displayed comparable values among meadows, marked spatial differences were observed for mean abundances (**Tab.1**). Indeed, the abundances of macrofauna were seven fold greater in the most densely populated meadow (Dinard) relative to the most sparsely populated meadow (Ile d'Yeu). Similarly, when core and edge samples within a meadow were averaged, significant differences were observed for both abundance and richness among meadows (**Fig. S1.2**). Chausey and Ile d’Yeu showed significantly lower average abundance values than other meadows. However, Chausey showed greater total species richness than other meadows (**Fig. S1.2**). Finally, we found no significant difference in abundance, richness or Simpson diversity among quadrats sampled in the core or edges of the meadows except for Ile d’Yeu. In Ile d’Yeu, core quadrats had significantly higher values of richness and Simpson diversity than edge quadrats. Finally, significant spatial differences were observed in the relative abundances of polychaetes, gastropods and bivalves and the contributions of these three groups to overall species richness across the five studied meadows. Chausey, Dinard and Ile d’Yeu had higher abundances of bivalves, Arcachon of gastropods, and Sainte-Marguerite of polychaetes (**Fig. 2**). In most meadows, polychaetes, gastropods and bivalves contributed similarly to the total richness, except for Sainte-Marguerite where the relative percentage of polychaetes was greater than that of gastropods and bivalves (**Fig. 2**). However, only six taxa appear to be strongly associated with the presence of *Zostera marina* and were found in all five sampled meadows (**Fig. S2.2**).

Variation in taxonomic and functional compositions (β-diversity)

Changes in polychaete, gastropod and bivalve composition associated with both cores and edges of the eelgrass meadows showed strong site-specific differences (**Fig. 3 A**). PCA axis 1 (20.5% of total variability) discriminated sites based on the bivalve composition, with the Dinard meadow showing the highestmollus diversity of bivalves and the greatest abundances in species *Loripes articulatus, Lucinoma borealis* and *Tricolia pullus*. PCA axis 2 (16.6% of total variability) discriminated sites based on the gastropod and polychaete compositions, with the Sainte-Marguerite meadow exhibiting the highest abundances of polychaetes such as *Platynereis dumerilii* or *Spio* cf. *martinensis* in contrast with the Arcachon meadow which exhibited the highest diversity and high of gastropods abundances of species such as

Jujubinus striatus and *Bittium reticulatum* (**Fig. 3B**). Finally, when considering the site presence/absence data independently, the core and edge modalities showed differences in terms of species composition (**Fig. S3.2**).

A functional analysis of assemblages gave a complementary vision of the structure of benthic macrofauna. Positive values of PC1 represented the abundance of small suspension feeders and surficial modifiers with medium life span as found in Dinard and Ile d'Yeu meadows, and negative values of PC1 represented greater abundance of larger biodiffusors and upward/downward conveyors with short life spans, as found in Sainte-Marguerite meadow. PC2 was primarily related to greater abundance of very small free-living grazers with little effect on bioturbation, as found in the Arcachon meadow (**Fig. 4**). However, presence/absence of the trait modalites within the sites did not show any differences in the functional composition among meadows nor between core and edge modalities (**Fig. S4.2**).

When considering the different components of *β* diversity using Jaccard's dissimilarity decomposition, polychaete, gastropod and bivalve communities sampled within a meadow shared on average 34.7% (± 12.8%) of species, compared to higher compositional differences observed among meadows, which shared on average only 13.0% of species (± 8.1%). Within-site comparisons had always two-fold greater similarity than between-site comparisons, indicating consistently greater variation in species composition from meadow to meadow. On average, when considering pairs of assemblages (samples) within a site, 65% of the species were found in only one assemblage: 56% of species changed in terms of identity (turnover) and 10% of differences were due to nestedness **(Fig. 5**; Within site). For pairwise comparisons among assemblages from different sites, differences were even more pronounced, with an average of 87% of species being found in only one assemblage, 83% of which was due to turnover and 4% to nestedness (**Fig. 5**; Among site). Overall, variation in species composition within and between sites were primarily due to changes in species identity. Functional β-diversity values for macrofauna associated with *Z. marina* also showed greater functional similarity within sites (67 ± 27 % ; **Fig. 5**) than among meadows (53 ± 27 %; **Fig. 5**). The relatively high levels of similarity in functional traits within and among meadows, indicates high levels of overlap in functional space. Functional β-diversity was mostly driven by nestedness (i.e. difference in the volume of the functional space filled by the assemblages; 22 ± 23 % within site and 32 ± 30 % among site; **Fig. 5**) rather than by turnover (i.e. functional spaces not shared by the two assemblages; 10 ± 20 % within site and 15 ± 18 % among site; **Fig. 5**).

Variation in community structure in relation to environmental conditions and morphological characteristics of the meadows

Overall, the pSEM models provided a good fit for the data (AIC= 169.623, $\chi2$= 67.623, p = 0.686, **Fig. 6**). At the regional scale, Δ water level had the greatest effects on assemblage composition, having direct effects on PC1 (positively correlated with bivalves, β= -0.85, $p < 0.0001$) and PC2 (positively correlated with gastropods, β= -1.70, $p < 0.0001$). Assemblage composition was also strongly correlated with temperature and current velocity, having direct negative correlations with bivalves (PC1, 0.38, $p < 0.0001$ and 1.02, $p < 0.0001$ respectively) and direct negative correlations with gastropods (PC2, β= -1.34, $p < 0.0001$ and 0.23, $p < 0.0001$ respectively). Similarly, mean sediment coarseness (D50) and mud content was also directly correlated with polychaetes (PC2, 0.38, $p < 0.0001$, 0.30, $p < 0.0001$). Indirect effects of environmental variables were also observed on assemblage compositions: temperature had indirect effects on bivalves (PC1, β= -0.15, $p < 0.02$) mediated by their effects on below-ground biomass. Therefore, the indirect effect of temperature enhanced its direct effect on PC1. At the local scale, diversity indices identified a different set of conditions and more cascading effects of the environment mediated by eelgrass trait responses (**Fig. 6**). The Δ water level had the greatest effects on richness, having positive direct effects on species richness (β= 1.00, $p< 0.0001$) and functional richness (FRic, β= 0.98, $p< 0.0001$). Species richness was also positively correlated with temperature (β= 0.39, $p< 0.02$). Indirect effects of environmental variables were also observed on local diversity indices: temperature, Δ water level and current velocity had indirect effects on species richness abundance and FRic mediated by their effects on leaf width and length. Because of these indirect effects on species richness, the direct positive effect of temperature and Δ water level was attenuated. Abundance and richness was also correlated with PC1 and PC2, showing direct positive correlation with polychaetes and bivalves, respectively. Morphological characteristics of the eelgrass beds had overall weaker effects on assemblage composition at regional scale than environmental variables, but had greater effects on species richness abundance and FRic. All coefficients and their associated p-values for the SEMs model are presented in **Table S3.2**.

Discussion

Eelgrass engineers highly productive habitats providing physical structure in sedimentary bottoms, enhancing community diversity and biomass, as well as affecting ecological key functions such as primary and secondary production (Boyé et al., 2019; Duffy, 2006b; Kenneth L. Heck et al., 2008). Here we examined multiple facets of biodiversity in five meadows spanning ~800 km of the Atlantic coast of France in order to better understand the factors that explain community diversity associated with eelgrass at different spatial scales.

Processes underlying local diversity

The foundation species *Z. marina* tends to have positive effects on the diversity and abundance of its associated organisms (Boström et al., 2006). Data collected for the five sites studied here showed that at the local scale, the number of polychaete, bivalve and gastropod species, and in particular their abundances, were significantly greater in meadows when compared to nearby bare sediments in nearly all sites. On average less than 15% of the species were found only in the bare sediments, while more than 60% were unique to meadows. Eelgrass has been shown to favor high levels of species richness and densities throughout its distribution (Orth, 1977; Edgar et al., 1994; Fonseca et al., 1990; Fredriksen et al., 2010; Orth et al., 1984; Stoner, 1980; Törnroos et al., 2013). This is likely due to a variety of trophic resources being available in meadows, such as epiphytes on eelgrass leaves or the accumulation of organic matter in meadows (Hemminga & Duarte 2000, Duffy 2006). In addition, meadows promote greater sediment stability, which may favor the colonization and accumulation of species (Boström et al., 2010; Fonseca & Fisher, 1986; Evamaria W. Koch & Verduin, 2001). Habitat complexity associated with eelgrass also results in enhanced shelter provisioning and lower predation (Kenneth L. Heck & Orth, 2006), favoring higher species abundances. Our results confirm that eelgrass meadows, like other bioengineered habitats, support greater species richness than geogenic habitats (Boyé et al., 2019; Henseler et al., 2019; Jones et al., 2018), and are thus of high conservation value (Boström et al., 2011; Boyé et al., 2019; Whippo et al., 2018).

Marine habitats are often spatially heterogeneous and habitat edges (vs. core) may have significant effects on population dynamics, community structure, and species diversity (Barnes & Hamylton, 2015; Bologna & Heck, 1999; Boström et al., 2011; Hovel et al., 2002; Wong & Dowd, 2015). *Z. marina* meadows are dynamic habitats that are constantly evolving in space and time (Clarke, 2019; Ferguson et al., 1993; Ferguson & Korfmacher, 1997; Robbins, 1997; Ward et al., 1997). However, some sectors of the meadows appear to be more stable over time (here called the core of the meadow), while environmental disturbances may lead other sectors of the meadow to be ephemeral (here termed edges). Since meadows can only exist in areas with soft bottom sediments, changes in substrate or topography can affect their distribution and productivity. The sedimentary environment can be altered by various processes such as wave disturbance due to strong storms (Koch, 2001; Reusch & Chapman, 1995), mobile dune migration caused by the prevailing coastal current (Marba & Duarte, 1995), and siltation due to sediment discharge in estuarine systems (Terrados et al., 1997). The mechanical effects of wave action on the sediment may be responsible for the loss of habitat where the more exposed parts of a meadow transition to bare sediment via the uprooting of shallow rhizomes (Fletcher & Fletcher, 1995; Kirkman & Kuo, 1990; Orth et al., 2006), while an increase in sediment input may bury the meadow (Terrados et al., 1997). Habitat edges may have impoverished communities as a result of instability or they may be ecotones (transition zones between meadows and bare sediment) that harbor species from both habitats, thus having higher diversity (Arponen & Boström, 2012; Fahrig, 2020; Fahrig et al., 2019; Kark & van Rensburg, 2006). In this study, faunal assemblages found in the core or edges of the meadows did not show strong differences in richness or abundance, although the cores of some meadows tended to have greater diversity or richness (but none showed both). Studies that examined fine-scale differences in diversity within meadows did not identify any consistent trend when comparing core and edge sectors, with most taxa showing no significant edge responses. (Boström et al., 2011). However, peracarid crustaceans consistently showed greater densities along edges compared to interior parts of a patch or meadow (Boström, 2006; and references therein) and fish also showed higher abundance and/or richness in meadow edges (Boström et al., 2011). In contrast, infaunal assemblages have generally shown no significant differences in diversity when comparing habitat cores and edges (Bowden et al., 2001; Tanner, 2003; Turner et al., 1999). Taxa with high mobility may respond differently to habitat edges than less mobile species. In our study, polychaete, gastropod and bivalve assemblages, three largely infaunal groups, showed no difference in trait composition, nor proportions of mobile species at meadow edges. The absence of highly mobile species in our dataset may therefore partly explain why no differences in abundance or richness were detected between the core and the edges of the meadows. Infaunal communities may be less affected by differences in predation pressure, predation avoidance, or other factors prevalent in edges which may have stronger effects on mobile fauna (Frost et al., 1999). In sum, at the local scale, community diversity and abundance were strongly favored by the presence of meadows over bare sediment, but meadow modality (core or edge) did not have a strong effect on the communities studied here, suggesting that ephemeral patches of eelgrass may provide similar benefits to biodiversity as stable cores.

Taxonomic and functional diversity at the regional scale

Significant spatial variation was observed in assemblages from the five meadows studied here. Taxonomic differences among sites were accompanied by changes in the abundances of specific trait combinations. The Dinard meadow was rich in bivalves and characterized by high abundances of small suspension feeders, the Sainte-Marguerite meadow by greater abundances of small to large bio diffusers and upward/downward conveyors, most of which were polychaetes, and the Arcachon meadow by greater abundance of very small free-living grazers with little effect on bioturbation (gastropods). The Chausey meadow was not characterized by any specific trait combinations, but rather a combination of all the traits found in the other meadows. In our analysis of Jaccard dissimilarity, high taxonomic turnover was observed among meadows, with taxonomic turnover being often > 70%, while functional turnover was only 10% on average. Previous observations have shown significant variation in species composition among meadows, confirming that the faunal composition of meadows is not a fixed or constant attribute (Henseler et al., 2019; Törnroos et al., 2013; Wong & Dowd, 2015). Despite significant changes in community composition among sites, species nestedness remained within a narrow range. This indicates that changes in species composition were mostly driven by simultaneous species gains and losses with richness remaining comparable from meadow to meadow. The narrow range of species richness described in these meadows would therefore correspond to the carrying capacity (*sensu* Hansen et al., 2011) of species richness for eelgrass (Boyé et al., 2017). High taxonomic turnover may indicate a large number of transient species, either observed in one meadow but not another by chance, or present only for a given amount of time (Boyé et al., 2019; Umaña et al., 2017). This spatial dynamics appears to create source-sink dynamics involving interactions among local communities at larger scales, allowing the persistence of many species that disperse from nearby habitats (Hillebrand et al., 2008; Leibold et al., 2004). Meadows, which are sink areas, provide refuge for larvae and organisms in more exposed environments such as bare sediments (Bostrom & Bonsdorff, 2000; Bouma et al., 2009). The high species replacement as well as high levels of overlap in functional space may indicate that the studied meadows share essential properties in terms of resource availability despite varying local conditions (Boyé et al., 2017; Cornell & Lawton, 1992). However, resource-rich environments can favor species with certain traits when competition is focused on limiting resources (Boyé et al., 2019; Perronne et al., 2017; Wong & Dowd, 2015). Epiphytes present on *Z. marina* leaves or the amount of detrital material feeding the food webs of meadows

(Ouisse et al., 2012) may act as a central resource leading to the observed difference in dominance of grazers, suspensory sessile microphages, or species with upward and downward transport activity (Boyé et al., 2019). Here we showed the importance of considering multiple components of diversity and especially β-diversity patterns to fully understand meadow richness at broad spatial scales.

Link between environmental variables and meadow characteristics in structuring communities at different scales

At local scales, parameters that describe meadow complexity (e.g. biomass, LAI, shoot density) have been shown to directly influence species-level responses (e.g. growth, mortality, predation, movement, reproduction; (Boyé et al., 2022; Fonseca & Bell, 1998; Koch, 2001; Robbins & Bell, 2000). However, the relative importance of different biotic and abiotic factors in explaining the variability and diversity of communities associated with eelgrass at the regional scale has proven more difficult to understand because they typically covary (Bowden et al., 2001; Hovel et al., 2002; Turner et al., 1999). Our pSEM model has helped to clarify the relative contribution of certain parameters that influence community composition, as well as taxonomic and functional diversity in eelgrass, as has been determined for other foundation species (Lamy et al., 2020; Miller et al., 2018). The pSEM shows that differences in faunal assemblages at the regional level are primarily explained by direct effects of the environment, particularly by positive relationships of temperature and Δ water level on the relative proportions of bivalves and gastropods. Current velocity had a significant negative direct effect only on the relative proportion of bivalves, while sediment coarseness and mud content favored polychaete assemblages. Temperature and Δ water level were therefore the main drivers of assemblage in the meadow of Arcachon and Dinard, characterized by high abundances of gastropods and bivalves respectively. Sediment coarseness and mud content were the main drivers of diversity in a meadow such as Sainte-Marguerite which was rich in polychaetes or Ile d'Yeu which presented species specific to certain types of sediment as the genus *Magelona*. In general, polychaete assemblages appear to be primarily controlled by sediment stability and composition, as observed in previous studies (Bostrom & Bonsdorff, 2000; Boström & Bonsdorff, 1997; Bowden et al., 2001).

Environment was also found to affect assemblages indirectly via modification of meadow characteristics. The only significant cascade pathway involved the indirect influence of temperature on the relative proportion of bivalves, mediated by below-ground biomass. Thus, temperature had a very positive total effect, when its direct and indirect effects were combined. Water level and current velocity only had small effects on canopy structure, with low water level fluctuation and higher current velocity favoring greater leaf width. The pSEM results are at odds with previous findings that showed that low water level fluctuation favored canopy height (leaf length) to obtain light for photosynthesis (Larkum et al., 2006), or that areas with greater wave exposure tended to have increased below-ground biomass for stability (Fonseca & Bell, 1998). Rather, temperature had greater effects on leaf length and below-ground biomass in our study sites. The southernmost meadow of Arcachon had significantly higher temperatures and lower water level variations than all other sites, which may explain the particular canopy structure of this meadow having very long and wide leaves coupled with low shoot density as a result of these environmental conditions. While hydrodynamics have been considered to have a strong influence on meadow structure (Fonseca & Bell, 1998; Schmidt et al., 2011), our results only showed a regional effect for below-ground biomass, but not for canopy height or shoot density. One possible explanation is that variation within sites was too great to establish regional effects. Strong variability among eelgrass meadows has been reported for in the Atlantic coast of France, including inter-annual variability within the same site (Boyé et al., 2022). Our study considered a single season of a particular year, which may not have captured all of the possible environmental drivers that influence community structure in eelgrass.

In contrast to community composition, the pSEM did show that meadow characteristics affected taxonomic and functional diversity indices locally, but these were primarily explained as by indirect effects of the environment (temperature, water level and current velocity). Leaf width had positive effects on species abundances, taxonomic richness, functional richness, and to a lower extent, on functional evenness. Leaf length also had positive effects on all of these diversity metrics, except for functional evenness, and belowground biomass has moderate effects on abundances. Species richness and abundance has often been related to variation in eelgrass aboveground structure (Attrill et al., 2000; Leopardas et al., 2014). An increase in leaf area (such as broad rather than long leaves) may favor a greater presence of epiphytes and diatoms, thus favoring species such as the mesograzer (Fredriksen et al., 2005) or species such as the tube-building polychaete *Platynereis dumerilii* commonly found on *Zostera* leaves (Jacobs & Pierson, 1979). It also favors the presence of species from adjacent habitats (e.g. *Pusillina inconspicua* or *Musculus costulatus*; (Rueda et al., 2008), including species that use the eelgrass bed as a foraging and spawning site (e.g. Rueda et al., 2008). Similar trends in the effect of leaf area on species richness, diversity, and total abundance have been recorded in other eelgrass beds (Guidetti et al., 2002; Jacobs et al., 1983; Laugier et al., 1999; Rueda et al., 2008). Some studies suggest that eelgrass invertebrates may not respond to habitat complexity directly (Attrill et al., 2000) but rather to increased food availability in eelgrass beds (Bologna & Heck, 1999). Accumulation of detrital material such as drift algae as commonly observed in the St. Margaret's meadow (Boyé et al., 2019), may explain why this meadow was rich in polychaetes as *Spio* cf. *martinensis*. In our study, we did not quantify epiphytic or detrital biomass, only organic matter present in the sediments. Incorporating these additional parameters in future work, may help to explain additional factors that affect biodiversity associated with eelgrass, not accounted for here. Nevertheless, the pSEM allowed us to disentangle the influence of the multi-scale approach and quantify the biotic and abiotic factors that drive biodiversity in eelgrass (Lefcheck et al., 2015).

Conservation and management action

The results presented here have implications for future conservation of eelgrass meadows. Our results did not show strong differences in diversity or community composition between stable cores or unstable edges of eelgrass beds.

Future management may therefore not need to consider age or density of patches, and may not need to prioritize protection of different sectors of meadows (such as old stable cores). Our results indicate that once eelgrass becomes established, its positive effects on abundance and diversity of the fauna are quickly established as well; therefore, protecting any modality of eelgrass may provide benefits to protecting biodiversity. Eelgrass meadows are dynamic habitats that may expand or recede over annual or pluriannual cycles - but this may not necessarily be cause for concern (unless receding cycles do not reverse), because the diversity of associated communities appears to be established quickly. Finally, these results also show that meadow traits such as density, aboveground biomass may not necessarily provide good proxies for diversity of the fauna associated with eelgrass. Conservation programs aiming to protect biodiversity should therefore not rely on these kinds of morphological metrics as a replacement for estimates of faunal composition. In addition, management that focuses on protecting eelgrass because of its positive effects on biodiversity should also consider protecting adjacent habitats, and not only biogenic habitats, but also homogeneous or bare sediments or substrates. Management may need to consider protecting whole ecosystems, which may include a diversity of habitats found in a given region in order to maximize its benefits to protecting biodiversity and associated services. Conservation plans that aim at protecting marine habitats as ecosystems may therefore benefit from spatial mapping and monitoring. Mapping will help identify habitats of special interest like eelgrass but also adjacent habitats that also serve as sources of biodiversity that ultimately seek protection in eelgrass. Mapping that takes place at regular intervals may also help alert drastic changes in meadow size or receding cycles that do not reverse.

Finally, this study demonstrated that the geographic distribution of the meadows at the regional scale had stronger effects of benthic community composition, with only small effects of the structural characteristics of the meadows. Meadows appear to harbor subsets of species observed at regional scales, and patterns of community diversity are consistent with the spatial distribution of the meadows, rather than with meadow-scale dynamics. These patterns may be indicative of a metacommunity system and suggest that the processes that maintain diversity in meadows may reflect a seascape composed of many habitats connected by source-sink dynamics. If this is the case, conservation of eelgrass systems will require a spatially diverse network approach that preserves many habitats rather than considering meadows only.

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DATA AVAILABILITY STATEMENT

All data are available in SEANOE (https://www.seanoe.org/html/request/87709/57jfKFL2hyXopBVXNiMv/93250.zip).

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

BIOSKETCHES

Alexandre Muller is a PhD student in marine sciences at the Université de Bretagne Occidentale. He is also a member of the LEBCO team at the DYNECO laboratory at ifremer in Brest, France. His main research interests are in the macroecology of marine benthic communities, with a particular interest in the role of ecosystem engineers in the spatial variability of communities. He uses numerical ecology tools to explore the multiple facets of biodiversity and their underlying processes across spatial scales.

TABLES

Table 1: *Spatial variability of species richness, Simpson's index and abundance per m² for Zostera marina meadows at five sites located in metropolitan France. Mean values are displayed with their standard deviations. Values in bold indicate the number of species*

unshared with the other modalities of the site. Different letters indicate significant differences at Tukey's test ($p < 0.05$)

Sites	**Modality**	**Total species richness**	**Mean species richness**	**Mean simpson diversity**	**Mean abundance per m2**	**Mean FRic**	**Mean FEve**
Chausey	Bare sediment	13 - ***5 (7%)***	4 ±4 ^{A}	0.50 ±0.3 ^{A}	322 ±527 ^{A}	0.13 ±0.19 ^{A}	0.62 ±0.1
	Meadow	65 - **57 (81%)**	17 ± 4 $^{B, 2}$	0.83 ±0.04 ^{B}	2483 ±838 $^{B, 1}$	0.59 ±0.13 $^{B, 2}$	0.72 ±0.05 ^{13}
	Core	41 - ***15 (21%)***	15 ±2	0.84 ±0.03	2384 ±836	0.58 ±0.15	0.71 ± 0.04
	Edge	50 - ***23 (32%)***	19 ±4	0.83 ±0.1	2582 ±906	0.60 ±0.11	0.72 ±0.05
Dinard	Bare sediment	31 - ***11 (19%)***	11 ±8 ^{A}	0.67 ±0.35	1004 ±843 ^{A}	0.38 ±0.23 ^{A}	0.75 ±0.07 ^{A}
	Meadow	46 - **26 (46%)**	16 ±4 $^{B, 2}$	0.69 ±0.9	5835 ± 1577 $^{B, 1}$	0.61 ±0.12 $^{B, 2}$	0.62 ±0.06 $^{B, 23}$
	Core	32 - ***6 (10%)***	18 ±2	0.74 ±0.04	6189 ±898	0.63 ±0.08	0.65 ± 0.05
	Edge	40 - ***11 (19%)***	14 ±5	0.64 ±0.1	5482 ±2089	0.60 ±0.15	0.58 ±0.05
Sainte Marguerite	Bare sediment	22 - ***11 (23%)***	8 ±2 ^{A}	0.53 ±0.17 ^{A}	2729 ±2105 ^{A}	0.28 ±0.04 ^{A}	0.60 ±0.16
	Meadow	37 - **26 (54%)**	13 ±3 $^{B, 2}$	0.71 ±0.14 ^{B}	4550 ±2038 $^{B, 1}$	0.46 ±0.18 $^{B , 2}$	0.61 ±0.11^{2}
	Core	28 - ***8 (17%)***	14 ±2	0.65 ±0.15	5763 ±976	0.51 ±0.19	0.59 ±0.03
	Edge	28 - ***9 (19%)***	11 ±2	0.76 ±0.12	3338 ±2159	0.40 ±0.16	0.62 ±0.15
Ile d'Yeu	Bare sediment	8 - ***1 (3%)***	4 ±2 ^{A}	0.55 ±0.30	429 ±231	0.04 ±0.04	0.77 ±0.16

	Meadow	38 - **31** **(82%)**	8 ±4 $^{B, 1}$	0.69 ±0.18	774 ±449 ^{2}	0.22 ±0.18 ^{1}	0.73 ±0.14 ^{1}
	Core	34 - ***22*** ***(57%)***	11 ±4 ^{a}	0.78 ±0.11 ^{a}	1010 ±526	0.32 ±0.20 ^{a}	0.75 ±0.08 ^{a}
	Edge	16 - ***3*** ***(8%)***	5 ±1 ^{b}	0.59 ±0.2 ^{b}	537 ±181	0.12 ±0.10 ^{b}	0.72 ±0.19
Arcachon	Bare sediment	19 - ***5*** ***(10%)***	6 ±2 ^{A}	0.79 ±0.5	303 ±154 ^{A}	0.24 ±0.2 ^{A}	0.84 ±0.07 ^{A}
	Meadow	43 - **29** **(60%)**	14 ±3 $^{B, 2}$	0.70 ±0.15	5505 ±3787 $^{B, 1}$	0.65 ±0.08 $^{B, 2}$	0.63 ±0.08 $^{B, 123}$
	Core	32 - ***8*** ***(17%)***	13 ±2	0.64 ±0.2	5949 ±4305	0.56 ±0.1	0.61 ±0.08
	Edge	34 - ***7*** ***(15%)***	15 ±3	0.75 ±0.1	5061 ±3541	0.56 ±0.1	0.66 ±0.09

FIGURES

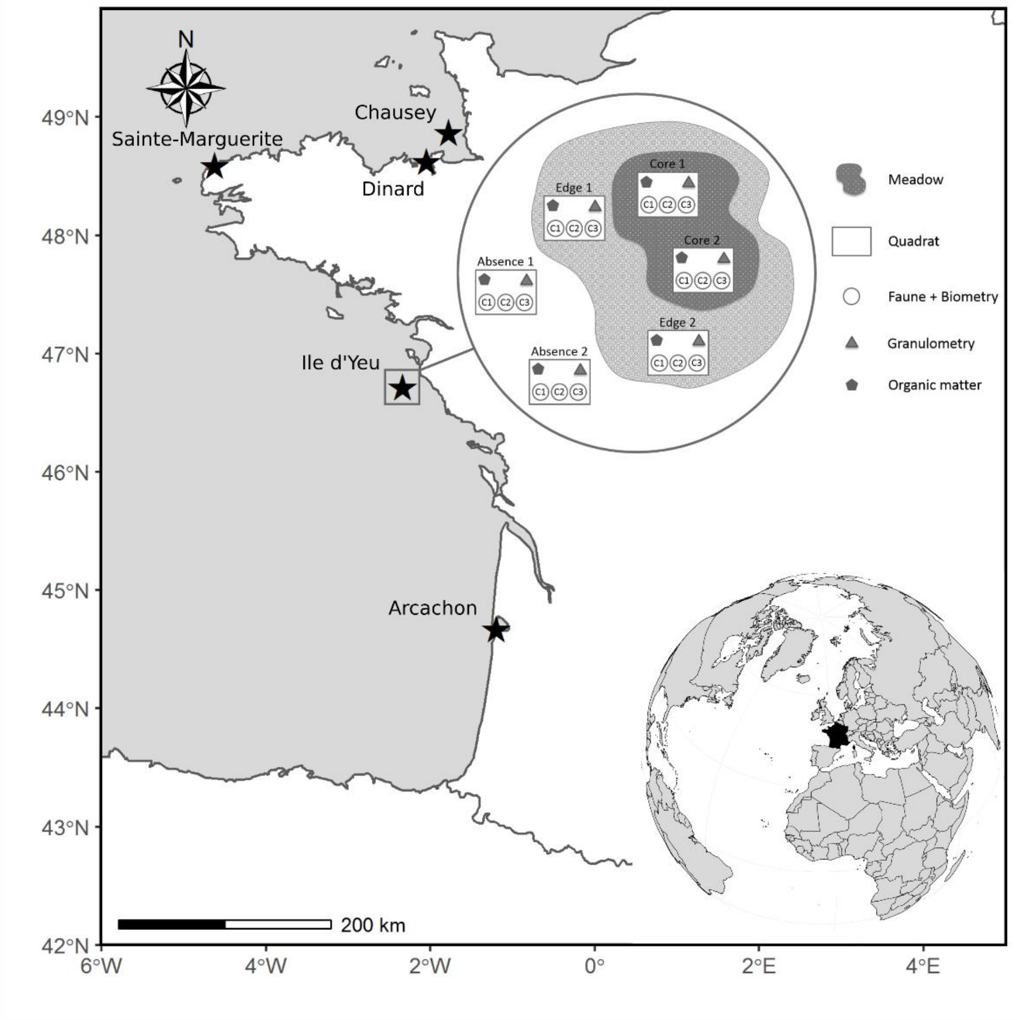

Figure 1. *Map indicating the locations of the 5 study sites of* Zostera marina meadows *in France: three in the The English Channel, and two in the Bay of Biscay. (All sites were sampled in six different stations).*

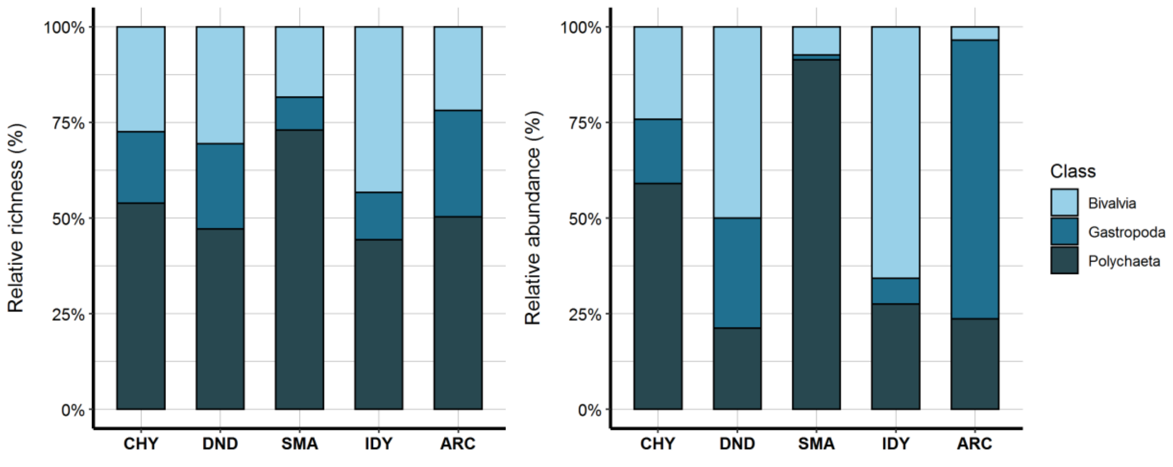

Figure 2. *Richness and density relative percentage of the different taxonomic groups present according to sites: Chausey (CHY), Dinard (DND), Sainte-Marguerite (SMA), Ile d'Yeu (IDY), Arcachon (ARC).*

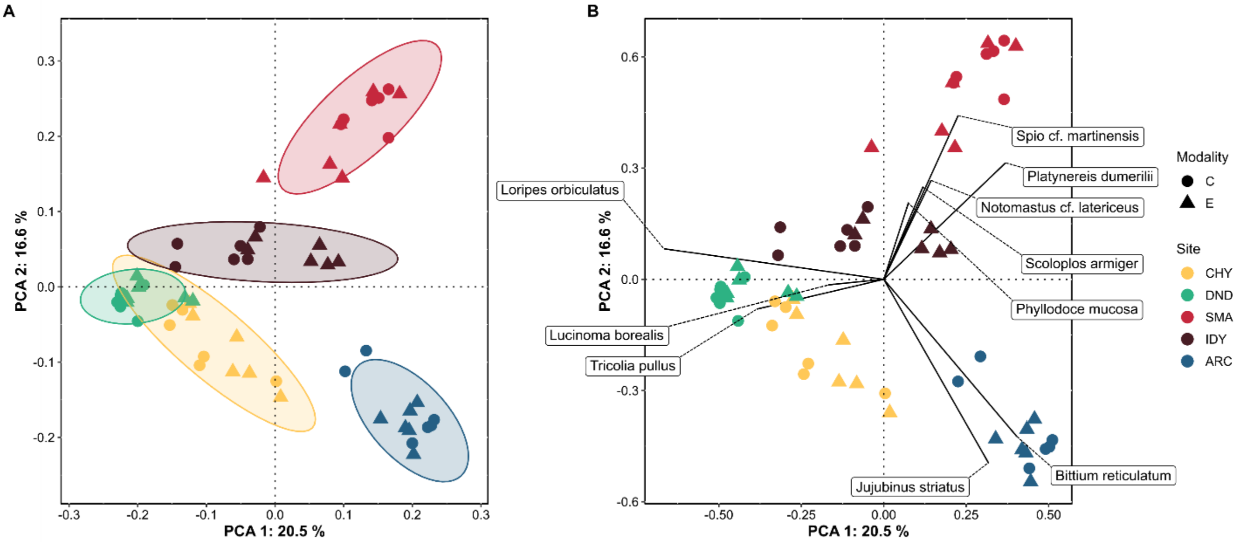

Figure 3. *Principal component analyses of the Hellinger-transformed abundances for total (A & B), mollusca (C & D), and polychaeta (E & F) fauna of the five Zostera marina beds sampled on two modalities, core and edge.* ***A.*** *the sites for each point sampled in core and edge with their 95% confidence dispersion ellipses, represented in scaling 1 (distance biplot) preserving the distances among the sites. Within-site dispersions represent variation of the communities among modalities.* ***B.*** *Positions of the species for which the two first axes represented at least 40% (cumulative R2) of their variance, represented in scaling 2 (correlation biplot) preserving the covariances among the species.*

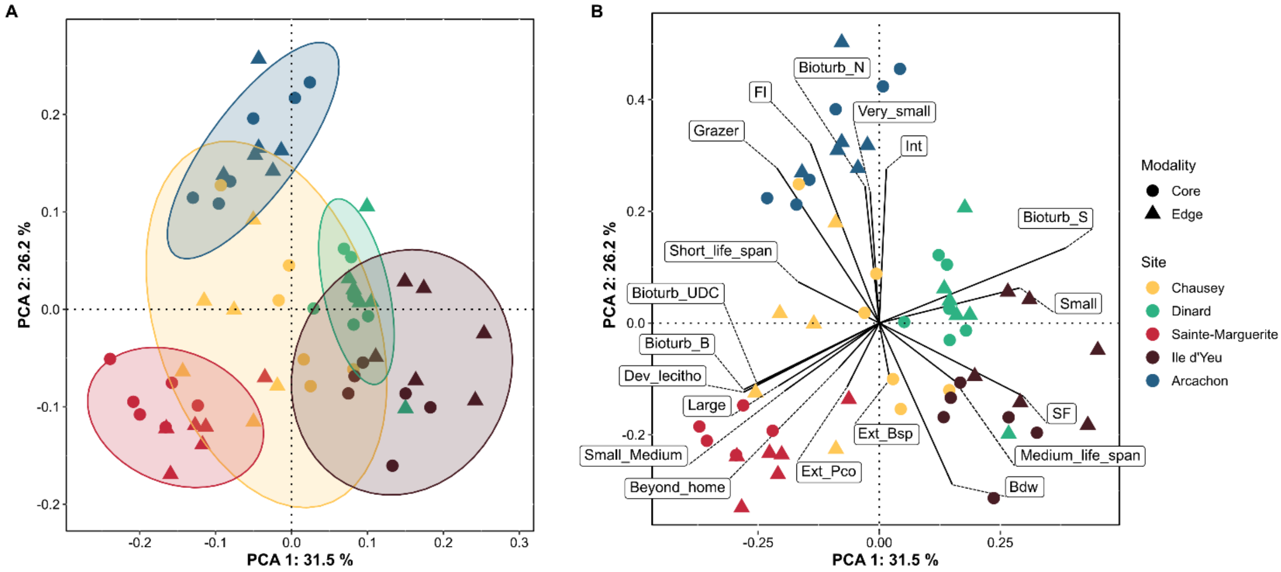

Figure 4. *Principal component analysis (PCA) of Hellinger- transformed trait modality abundances.* ***A.*** *the sites for each point sampled in core and edge with their 95% confidence dispersion ellipses, represented in scaling 1 preserving the distances among the sites.* ***B.*** *positions of the trait modality for which the two first axes represented at least 40% (cumulative R2) of their variance, represented in scaling 2.*

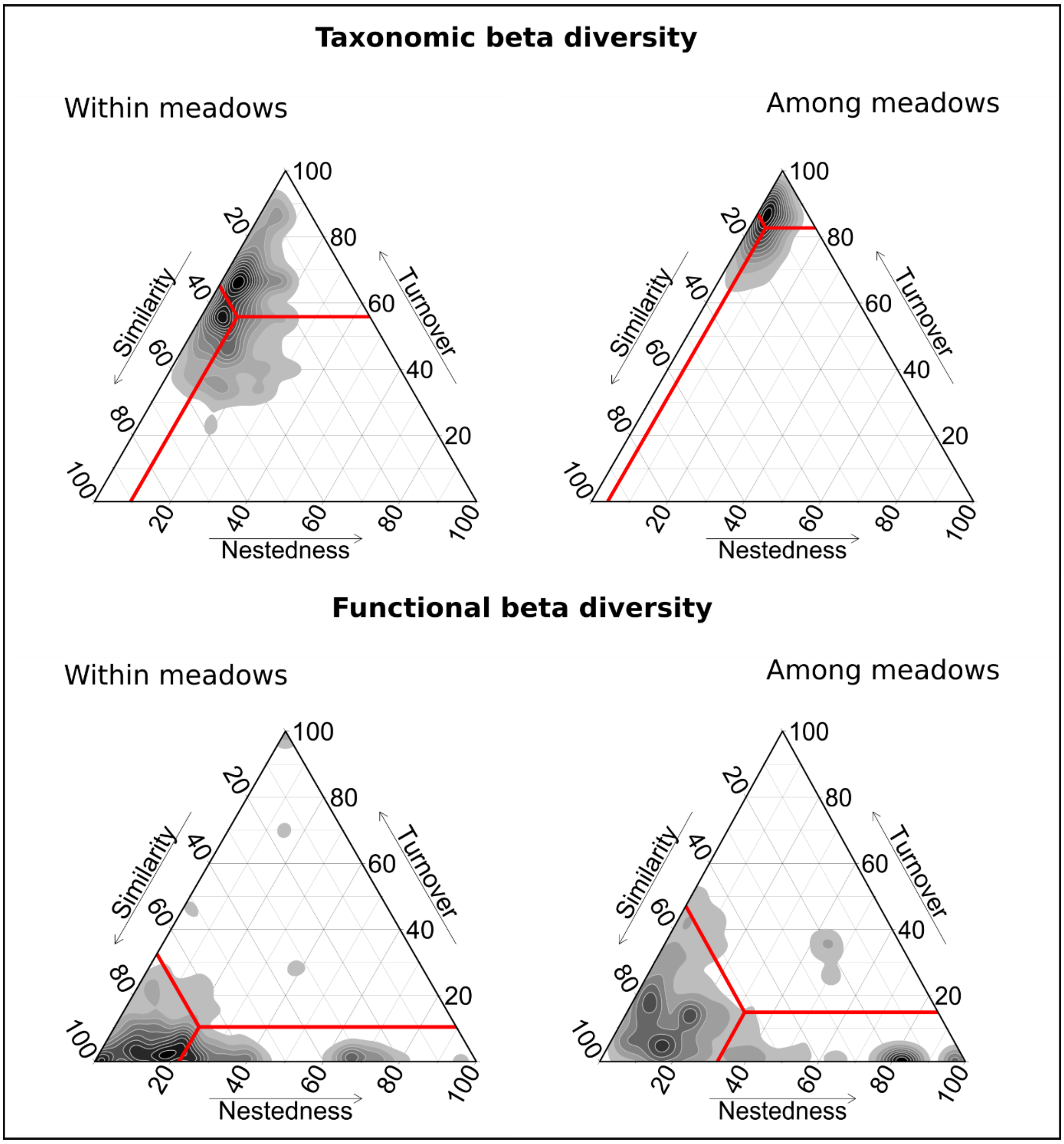

Figure 5: *Triangular plots illustrating the spatial variations of the taxonomic β-diversity. Sorensen dissimilarity between the species composition (presence/absence data) of the five seagrass beds was used to quantify their similarity, and the two components of their beta diversity nestedness (i.e. influenced by the difference in number of species between the two communities) and turnover (i.e. species replacement between two communities). Contributions were calculated separately, for comparisons between samples belonging: to the same meadow (within meadows), to different meadows (among meadows). Red lines indicate the centroid value for each graph with its associated mean values for the three components of dissimilarity.*

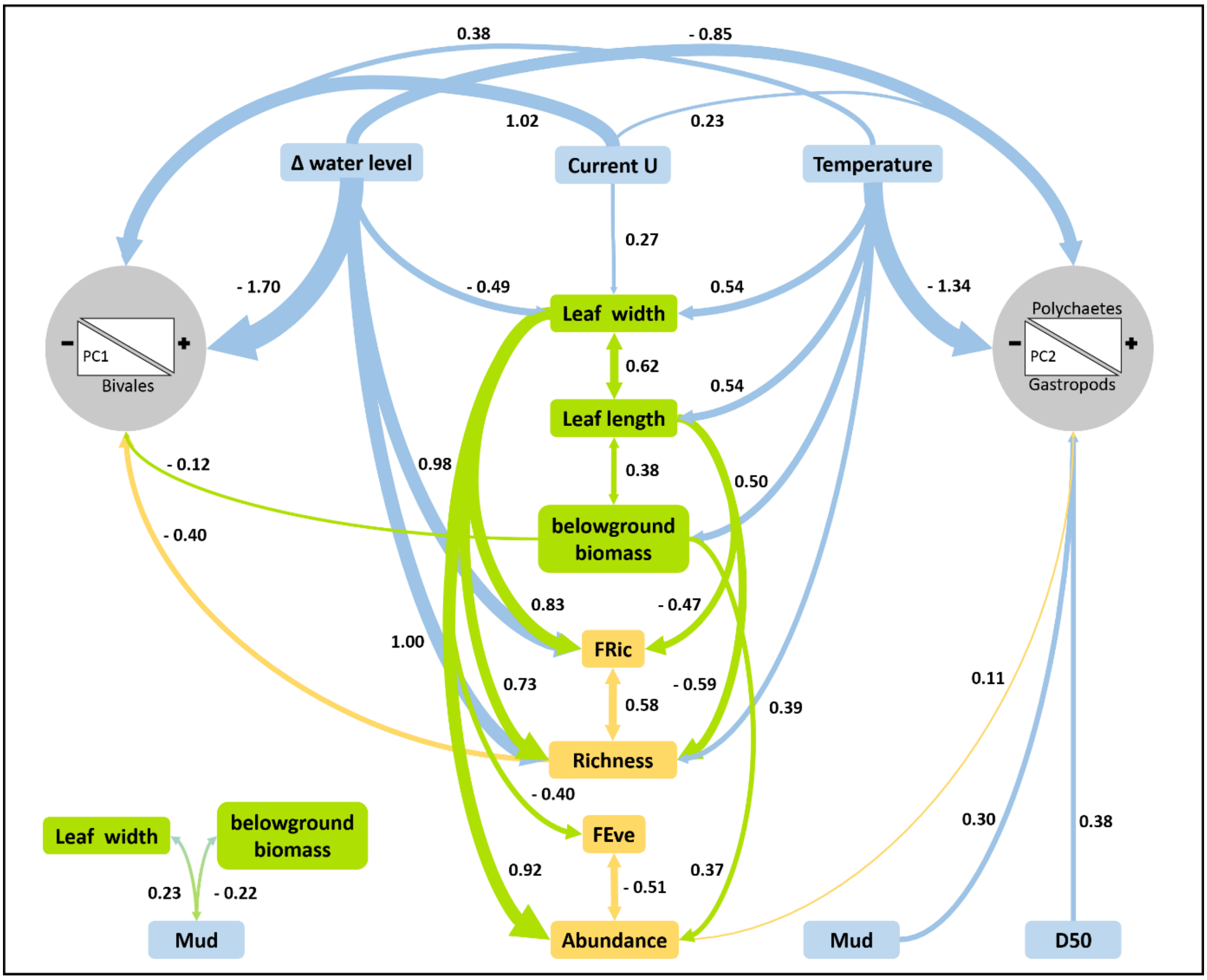

Figure 6: *Best model fitted with piecewiseSEM (structural equation modeling) describing the relationships among Zostera marina traits (in green) and environmental variables (in blue) on the principal component analyses of the Hellinger-transformed abundance (in gray). Arrows indicate directional effects. Arrow and dot lines indicate positive and negative relationships, respectively. Values over the lines denote the standardized effect size (regression coefficient) of each relationship. Nonsignificant relationships (P > 0.05) have been omitted for clarity (Table S3). Line thickness is proportional to the effect size. R^2: Belowground biomass= 0.25; PC1= 0.87; PC2= 0.93, Leaf length= 0.30; Leaf width= 0.72; Abundance= 0.39; Richness= 0.58; FRic= 0.57, FEve= 0.14.*