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1 **Title: Leaf size doesn't matter: environment shapes eelgrass**

2 **biodiversity more than a foundation species' traits.**

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12 Abstract

13 **Aim:** Understand the ecological processes that shape community composition in eelgrass

14 meadows along the coast of France at local and regional scales.

15 **Location:** Northeastern Atlantic.

16 **Methods:** Combining taxonomic and trait-based approaches with structural equation

17 modeling, we explored the mechanisms governing community assembly in five meadows

18 located over a distance of 800 km along the French coast in the Northeast Atlantic. We

19 assessed the spatial variability of eelgrass-associated invertebrate communities as affected

20 by environmental parameters or morphological traits of the eelgrass and linked these

21 mechanisms to their impacts at local and regional scales through analyses of the taxonomic

22 and functional α and β diversities. We then quantified the direct and indirect effects of

23 environmental factors on macrofaunal structure and composition.

24 **Results:** Eelgrass meadows locally favored higher species abundance, diversity, and

25 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

53 species from the regional pool leading to what is known as α-diversity (Crist & Veech, 2006;

54 De Troch et al., 2001; Sanders et al., 2007; Thompson et al., 2020; Whittaker, 1960, 1972).

55 Interactions between local and regional processes generate spatial gradients in community

56 structure known as β-diversity (Airoldi et al., 2008; Anderson et al., 2011; Thompson et al.,

57 2020; Whittaker, 1960, 1972). Examining each of these components of diversity is essential

58 for determining which factors most influence communities of a given habitat type.

59   It is now widely recognized that the integration of functional information based on

60 species traits provides a complementary understanding of community functioning along spatial

61 scales (Díaz & Cabido, 2001; Pavoine & Bonsall, 2011; Stegen & Hurlbert, 2011; Swenson et

62 al., 2011). Indeed, comparing taxonomic and functional diversity can provide insights into the

63 ecological processes that shape community composition (Mori et al., 2018; Swenson, 2011;

64 Villéger et al., 2010) and the impact of biodiversity loss on ecosystem functioning (Burley et

65 al., 2016; Cadotte et al., 2011). For example, trait homogenization within communities, when

66 only species with a specific set of traits are found under certain conditions, are indicative that

67 selective processes are at work, such as environmental filtering (Münkemüller et al., 2020;

68 Perronne et al., 2017). Comparing taxonomic and functional diversity (on the basis of

69 presence–absence and abundance data) can therefore provide key insights into the

70 mechanisms affecting biodiversity.

71   Differences in biodiversity among assemblages (β-diversity) can also be considered

72 as two separate components: species turnover (the replacement of species or functional

73 strategies in one assemblage compared to another) and nestedness (differences in richness

74 when one assemblage is a subset of another, (Baselga, 2010, 2012; Legendre, 2014; Villéger

75 et al., 2013). Quantifying the relative contributions of turnover and nestedness to β-diversity

76 can improve our understanding of the ecological processes that structure communities.

77 Indeed, two communities may have high taxonomic or functional β-diversity as a result of

78 different processes that can be disentangled by partitioning the variation into turnover and

79 nestedness. For example, high β-diversity may be due to high functional turnover, indicating

80 niche differentiation between communities (Loiseau et al., 2017; Villéger et al., 2013), while

3

81 high β-diversity could also result from high nestedness (accompanied then by low functional

82 turnover), if the species hosted by one community represent only a small subset of the

83 functional strategies present in the other community, indicating a different niche filtering

84 intensity (Loiseau et al., 2017; Villéger et al., 2013). It is therefore important to consider the

85 contributions of both turnover and nestedness in comparisons among communities.

86   Biodiversity is typically greater in structurally complex compared to homogeneous

87 habitats (Lapointe & Bourget, 1999; MacArthur & MacArthur, 1961). Many communities coexist

88 in habitats that have been modified by organisms that have critical effects on habitat structure

89 and ecosystem functions; these are called foundation species (Dayton 1972). Foundation

90 species not only complexify the habitat but also control the availability of resources for other

91 organisms (Ellison, 2019; Sarà, 1986). By modifying habitat, foundation species can influence

92 community assembly and its long-term persistence through numerous mechanisms such as

93 niche partitioning (Willis et al., 2005), altering competitive and predator-prey interactions

94 (Costello et al., 2015), or providing refuge from physical stressors (Bulleri et al., 2016; Jurgens

95 & Gaylord, 2018; Scheffers et al., 2014). Habitat complexity also favors microhabitat

96 heterogeneity (Bulleri et al., 2016; Lassau et al., 2005; Schöb et al., 2012; Williams et al.,

97 2002), which may attract or deter certain species thereby influencing local diversity (Swenson

98 & Weiser, 2010; Walters & Wethey, 1991; Wood et al., 2015). Because community composition

99 can vary greatly within habitats across environmental gradients (Boström et al., 2006; Boyé et

100 al., 2017), studying the effect of habitat structural complexity on the associated communities

101 improves our understanding of the processes structuring biodiversity over various geographic

102 scales (Airoldi et al., 2008). Foundation species are also likely to mediate the impact of climate

103 and anthropogenic change on biodiversity, particularly because they tend to buffer or attenuate

104 change (Bulleri et al., 2018; Sunday et al., 2017). While foundation species exert many direct

105 effects on the communities they support, less is known about the indirect effects that they or

106 the environment may exert on communities. For many foundation species, a comprehensive

107 understanding of the direct and indirect influences on biodiversity are lacking (Miller et al.,

108   2018), which limits our ability to in turn predict the cascading effects of anthropogenic and

109   climate change on associated fauna.

110   *Zostera marina* (Linnaeus, 1753) is a flowering marine plant that occurs from temperate

111   to subarctic regions (Short & Frederick, 2004), forming meadows that are recognized as being

112   among the most important coastal marine ecosystems on the planet (Costanza et al., 1997;

113   Dewsbury et al., 2016; Duarte et al., 2008; Duffy, 2006a). Eelgrass is a foundation species,

114   providing essential functions and services including coastal protection, erosion control, nutrient

115   cycling, water purification, carbon sequestration, as well as food and habitat for a variety of

116   species (Barbier et al., 2011; Cullen-Unsworth & Unsworth, 2013; Duarte, 2002; Fourqurean

117   et al., 2012; Healey & Hovel, 2004; K. L. Heck et al., 2003; Orth et al., 2006; Schmidt et al.,

118   2011). Eelgrass can have a strong influence on the spatial distribution of associated fauna by

119   altering the hydrodynamics of the marine environment (Fonseca & Fisher, 1986), providing

120   abundant resources, available surface area, and increased ecological niches. Meadows also

121   provide protection from predation by providing greater habitat complexity both above and

122   below-ground (Gartner et al., 2013; Kenneth L. Heck & Wetstone, 1977; Orth et al., 1984;

123   Reynolds et al., 2018). At the local scale, it is generally accepted that meadow complexity

124   parameters (e.g. biomass, shoot density, leaf length) directly influence species-level

125   responses (e.g. growth, mortality, predation, movement, reproduction). The variability of

126   eelgrass structure in relation to its physical environment is fairly well understood (Boyé et al.,

127   2022; Fonseca & Bell, 1998; Frederiksen et al., 2004; Robbins & Bell, 2000), as is the effect

128   of the environment on the community structure (Blake & Duffy, 2012; Douglass et al., 2010;

129   Yeager et al., 2019). However understanding how these components interact, and the relative

130   importance of different environmental and biotic factors in explaining biodiversity at multiple

131   spatial scales has proven more difficult (Bowden et al., 2001; Hovel et al., 2002; Turner et al.,

132   1999). Indeed most of the potential cascading effects studied to date involve the loss or

133   replacement of foundation species (Airoldi et al., 2008; Ellison et al., 2005; Pessarrodona et

134   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

189   three 0.03 m^2 manual push cores and placed into 1 mm nylon mesh collection bags, which

190   allowed pre-sieving and washing away most sediments directly in the field (**Fig. 1**). Once in

191   the laboratory, the content of each sample was preserved in 70% ethanol. To ensure optimal

192   species fixation, ethanol was replaced every 2 days, for a total of three renewals. In the

193   laboratory, cores were sieved on a 1 mm mesh. Macrofauna was then extracted from the

194   sediments and counted. All individuals belonging to polychaetes, gastropods and bivalves

195   were identified to the lowest taxonomic level possible, most often to the species level. All

196   species names were used according to the World Register of Marine Species and references

197   used for taxonomic identification are listed in **Appendix S1** in Supporting Information. To

198   ensure consistent taxonomic resolution across samples, a unique operator (A. Muller) was

199   involved and uncertain identifications were cross-checked by a taxonomic expert (G. Droual).

200   **Morphological and structural trait measurements**

201   All shoots in each sample were counted to measure *Z. marina* densities. Five shoots

202   were randomly selected for morphometric measurements, which included sheath height, leaf

203   length and width, and the number of leaves per shoot. Sheath height was measured from the

204   first node to the leaf separation mark. The length of each leaf was measured from the node

205   mark to the apex. The width was taken at mid-length. The biomass of leaves, sheaths, roots

206   and rhizomes were measured separately for each of the 2 core and 2 edge quadrats (i.e. a

207   total of 15 measurements in each quadrats) in each of the 5 sites, and were measured as dry

208   weight following 48 hours of desiccation at 60°C. Total biomass and densities were expressed

209   per square meter. To assess the relative investment of *Z. marina* between its above-ground

210   and below-ground compartments, we calculated the ratio between the biomass of leaves and

211   sheaths and the biomass of roots and rhizomes (Boyé et al., 2022). Average leaf, root and

212   rhizome biomass per shoot were estimated by dividing the total biomass by the shoot densities.

213   The Leaf Area Index (LAI) was then calculated as the ratio between the total leaf area of the

214   plant and the substrate area it covers. For all other variables (densities, sheath height, leaf

215   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

242   the harmonic components of tidal heights and currents computed from the MARS3D models

243   (https://marc.ifremer.fr/en; Le Roy and Simon, 2003) and the TidalToolBox (Allain, 2016). All

244   environmental variables are listed in **Tab. S1.2**.

245   **Biological traits**

246   To assess functional diversity, biological traits were scored for polychaetes, gastropods

247   and bivalves, three phylogenetically diverse groups composed of a large diversity of species

248   exhibiting a wide range of ecological strategies (Aldea et al., 2008; Gosling, 2015; Jumars et

249   al., 2015; Lassau et al., 2005; Teso et al., 2019). Eight biological traits (divided into 30

250   modalities) were selected (**Tab. S2.2**), providing information related to the ecological functions

251   performed by the associated macrofauna. These traits characterized the maximum size,

252   feeding and reproductive ecology, mobility, and bioturbation potential of the species (**Tab.**

253   **S2.2**) and were chosen to reflect key biological and ecological processes (Queirós et al., 2013;

254   Solan et al., 2004; Thrush et al., 2006). Species were scored for each trait modality based on

255   their affinity using a fuzzy coding approach (Chevene et al., 1994), where multiple modalities

256   can be assigned to a species if appropriate, and allowed for incorporation of intraspecific

257   variability in trait expression. A trait matrix containing total abundances of each modality by

258   sites was calculated using the matrix product of the site-species matrix with the species-trait

259   matrix, after normalizing scores to 1 per trait and species. Information for polychaetes was

260   primarily extracted from Fauchald et al (1979), Jumars et al (2015), and Boyé et al (2019).

261   Information for gastropods and bivalves was obtained either from biological trait databases

262   (www.marlin.ac.uk/biotic, www.univie.ac.at/arctictraits) or from publications (e.g. Bacouillard,

263   2019; Martini et al., 2020; Queirós et al., 2013; Thrush et al., 2006). Information was collected

264   at the lowest possible taxonomic level and when missing was based on data available in other

265   species of the genus, or in some cases, in the same family (only for traits with low variability

266   for these families).

267   **Statistical analyses**

268   We studied changes in total abundance, taxonomic and functional diversity across

269   different spatial scales, from within habitat modalities (edge *vs.* core) to local habitat conditions

270   (meadow *vs.* bare sediment) to regional habitat conditions (meadow *vs.* meadows) using three

271   different characterizing α-diversity measures. Taxonomic diversity was estimated using the

272   Simpson index for each modality in each site to characterize the α-diversity of polychaetes,

273   gastropods and bivalves and its spatial variation. The Simpson diversity index was chosen

274   because of its property of reducing the influence of rare species (Hill, 1973), to emphasize the

275   effect of species accounting for most of the total abundance. The functional structure of

276   polychaetes, gastropods and bivalves assemblages was characterized using two

277   complementary indices: functional richness (FRic) and functional evenness (FEve, Laliberte &

278   Legendre, 2010; Mouchet et al., 2010; Villéger et al., 2008). Differences between core vs edge

279   and meadow vs bar sediment were tested with two-way nested ANOVA and meadow vs

280   meadow were tested with one-way ANOVA. Pairwise comparisons were carried out with the

281   Tukey-test ($p < 0.05$).

282   Community structure associated with *Z. marina* among the five sites were compared

283   using Principal Component Analysis (PCA) of Hellinger-transformed species abundances for

284   polychaetes, gastropods and bivalves combined. Abundance based dissimilarities can be

285   strongly influenced by overabundant species or by a high proportion of rare species. Applying

286   a Hellinger transformation to abundance data allows Euclidean-based methods to be used,

287   while also not overweighting rare species (Legendre & Gallagher, 2001). In addition,

288   Sørensen's dissimilarity index (Sørensen, 1948) was calculated based on presence-absence

289   data for each community sample. For each pair of samples, taxonomic β-diversity and its two

290   components, turnover and nestedness, were computed using the Baselga partitioning scheme

291   (Baselga, 2017; Schmera et al., 2020). Functional β-diversity was computed based on fuzzy

292   correspondence analysis, where axes were synthetic components summarizing functional

293   traits (Mouillot et al., 2014; Villéger et al., 2011). The first two axes were used for calculating

294   the Jaccard's dissimilarity index according to Villeger's equation (2013) for all pairwise

295 comparisons between samples (1) belonging to the same site (within site), or (2) belonging to

296 different sites (among site).

297   A Redundancy analysis (RDA) was used to investigate to which extent species

298 composition was affected by two sets of predictors, namely on site environmental variables

299 and morphological and structural characteristics of *Z. marina*. Collinear variables were

300 removed using variance inflation factors (VIF) with a threshold of five as recommended in

301 Legendre & Legendre (2012), which resulted in the removal of some of the variables

302 characterizing the distribution of the sediment, salinity, dissolved oxygen and nutrients. Then,

303 a stepwise selection based on adjusted coefficients (R^2_{adj}) was applied to remaining

304 environmental variables and the morphological characteristics of *Z. marina* (Blanchet et al.,

305 2008). The results of the RDA were used to ultimately select six environmental and four

306 morphometric variables that most explained the variation in the community dataset (**Fig. S5.2**)

307 - which included: temperature, current velocity, Δ water level, mean grain size, mud content,

308 below-ground biomass, leaf width and leaf length. These variables were then used to construct

309 piecewise structural equation models (SEM, Lefcheck, 2016) to explore the direct and indirect

310 effects (through eelgrass trait responses) of environmental factors on the structure and

311 composition of the macrofauna. This technique allows fitting complex networks, facilitating the

312 identification of cascading effects (Airoldi et al., 2008; Barnes, 2017; Elbrecht et al., 2017;

313 Ellison et al., 2005; Lefcheck et al., 2015; Pessarrodona et al., 2019; Wernberg et al., 2012).

314 We implemented a model that considered the effects of environmental and morphometric

315 variables on regional gradients of taxonomic composition (using the first two axes of the PCA

316 on Hellinger-transformed abundances), and on local diversity indices (using total abundance,

317 species richness, FRic, and FEve).

318   All diversity and functional metrics calculations and statistical analyses were performed

319 using the G2Sd (Fournier et al., 2014), 'ade4' (Dray & Dufour, 2007), 'vegan' (Oksanen et al.,

320 2019), 'FD' (Laliberté et al., 2014), 'betapart' (Baselga, 2012) packages and multivariate

321 analysis in the form of piecewise SEM was conducted using the packages 'nlme', and

322 'piecewiseSEM' (Lefcheck et al., 2015) in R 4.0.3 (R Development Core Team, 2008).

Results

324   A total of 90 community samples were collected in the five sites, for a total of 9277

325 individuals and 138 species (56 molluscs and 82 polychaetes). Rare species accounted for a

326 large proportion of the samples: 43% of the species were observed in a single sample and

327 38% were represented by one or two individuals.

Spatial patterns of α diversity

329   The abundance and diversity of polychaetes, gastropods and bivalves differed among

330 core, edge and bare sediment modalities (**Tab. 1, Fig. S1.2**). Samples collected within the

331 meadows (core + edge) showed marked differences in community structure compared to bare

332 sediments: the mean abundance (ind.m^{-2}) and the average number of species was significantly

333 higher in meadows than in bare sediments at all localities, except Ile d'Yeu where abundances

334 in meadows and bare sediment were not significantly different (**Tab. 1**). Communities

335 associated with meadows showed greater variation in both mean abundance (2384 to 6188

336 ind.m^{-2}) and average number of species (11 to 19), than the more homogeneous bare

337 sediments (Ile d'Yeu excluded) which had a abundances of only 303 to 2729 ind.m^{-2} and 4 to

338 11 species (**Tab. 1**). Similarly when looking at functional diversity indices, bare sediments had

339 small, trait-poor functional space (low FRic) with evenly distributed abundances (high FEve).

340 In comparison, meadows had larger functional spaces (higher FRic) with abundances being

341 concentrated on a few traits (low FEve). This indicates that the dominant species shared the

342 same functional traits and that a large part of the functional space was occupied by less

343 abundant species with rarer traits.

344   In contrast to mean species richness and Simpson index, which displayed comparable

345 values among meadows, marked spatial differences were observed for mean abundances

346 (**Tab.1**). Indeed, the abundances of macrofauna were seven fold greater in the most densely

347   populated meadow (Dinard) relative to the most sparsely populated meadow (Ile d'Yeu).

348   Similarly, when core and edge samples within a meadow were averaged, significant

349   differences were observed for both abundance and richness among meadows (**Fig. S1.2**).

350   Chausey and Ile d'Yeu showed significantly lower average abundance values than other

351   meadows. However, Chausey showed greater total species richness than other meadows

352   (**Fig. S1.2**). Finally, we found no significant difference in abundance, richness or Simpson

353   diversity among quadrats sampled in the core or edges of the meadows except for Ile d'Yeu.

354   In Ile d'Yeu, core quadrats had significantly higher values of richness and Simpson diversity

355   than edge quadrats. Finally, significant spatial differences were observed in the relative

356   abundances of polychaetes, gastropods and bivalves and the contributions of these three

357   groups to overall species richness across the five studied meadows. Chausey, Dinard and Ile

358   d'Yeu had higher abundances of bivalves, Arcachon of gastropods, and Sainte-Marguerite of

359   polychaetes (**Fig. 2**). In most meadows, polychaetes, gastropods and bivalves contributed

360   similarly to the total richness, except for Sainte-Marguerite where the relative percentage of

361   polychaetes was greater than that of gastropods and bivalves (**Fig. 2**). However, only six taxa

362   appear to be strongly associated with the presence of *Zostera marina* and were found in all

363   five sampled meadows (**Fig. S2.2**).

Variation in taxonomic and functional compositions (β-diversity)

365   Changes in polychaete, gastropod and bivalve composition associated with both cores

366   and edges of the eelgrass meadows showed strong site-specific differences (**Fig. 3 A**). PCA

367   axis 1 (20.5% of total variability) discriminated sites based on the bivalve composition, with the

368   Dinard meadow showing the highestmollus diversity of bivalves and the greatest abundances

369   in species *Loripes articulatus, Lucinoma borealis* and *Tricolia pullus*. PCA axis 2 (16.6% of

370   total variability) discriminated sites based on the gastropod and polychaete compositions, with

371   the Sainte-Marguerite meadow exhibiting the highest abundances of polychaetes such as

372   *Platynereis dumerilii* or *Spio* cf. *martinensis* in contrast with the Arcachon meadow which

373   exhibited the highest diversity and high of gastropods abundances of species such as

14

374 *Jujubinus striatus* and *Bittium reticulatum* (**Fig. 3B**). Finally, when considering the site

375 presence/absence data independently, the core and edge modalities showed differences in

376 terms of species composition (**Fig. S3.2**).

377 A functional analysis of assemblages gave a complementary vision of the structure of

378 benthic macrofauna. Positive values of PC1 represented the abundance of small suspension

379 feeders and surficial modifiers with medium life span as found in Dinard and Ile d'Yeu

380 meadows, and negative values of PC1 represented greater abundance of larger biodiffusors

381 and upward/downward conveyors with short life spans, as found in Sainte-Marguerite meadow.

382 PC2 was primarily related to greater abundance of very small free-living grazers with little effect

383 on bioturbation, as found in the Arcachon meadow (**Fig. 4**). However, presence/absence of

384 the trait modalites within the sites did not show any differences in the functional composition

385 among meadows nor between core and edge modalities (**Fig. S4.2**).

386 When considering the different components of *β* diversity using Jaccard's dissimilarity

387 decomposition, polychaete, gastropod and bivalve communities sampled within a meadow

388 shared on average 34.7% (± 12.8%) of species, compared to higher compositional differences

389 observed among meadows, which shared on average only 13.0% of species (± 8.1%). Within-

390 site comparisons had always two-fold greater similarity than between-site comparisons,

391 indicating consistently greater variation in species composition from meadow to meadow. On

392 average, when considering pairs of assemblages (samples) within a site, 65% of the species

393 were found in only one assemblage: 56% of species changed in terms of identity (turnover)

394 and 10% of differences were due to nestedness **(Fig. 5**; Within site). For pairwise comparisons

395 among assemblages from different sites, differences were even more pronounced, with an

396 average of 87% of species being found in only one assemblage, 83% of which was due to

397 turnover and 4% to nestedness (**Fig. 5**; Among site). Overall, variation in species composition

398 within and between sites were primarily due to changes in species identity. Functional β-

399 diversity values for macrofauna associated with *Z. marina* also showed greater functional

400 similarity within sites (67 ± 27 % ; **Fig. 5**) than among meadows (53 ± 27 %; **Fig. 5**). The

401 relatively high levels of similarity in functional traits within and among meadows, indicates high

402 levels of overlap in functional space. Functional β-diversity was mostly driven by nestedness

403 (i.e. difference in the volume of the functional space filled by the assemblages; 22 ± 23 %

404 within site and 32 ± 30 % among site; **Fig. 5**) rather than by turnover (i.e. functional spaces not

405 shared by the two assemblages; 10 ± 20 % within site and 15 ± 18 % among site; **Fig. 5**).

406 **Variation in community structure in relation to environmental conditions and**

407 **morphological characteristics of the meadows**

408 Overall, the pSEM models provided a good fit for the data (AIC= 169.623, χ2= 67.623,

409 p = 0.686, **Fig. 6**). At the regional scale, Δ water level had the greatest effects on assemblage

410 composition, having direct effects on PC1 (positively correlated with bivalves, β= -0.85, p <

411 0.0001) and PC2 (positively correlated with gastropods, β= -1.70, p < 0.0001). Assemblage

412 composition was also strongly correlated with temperature and current velocity, having direct

413 negative correlations with bivalves (PC1, 0.38, p < 0.0001 and 1.02, p < 0.0001 respectively)

414 and direct negative correlations with gastropods (PC2, β= -1.34, p < 0.0001 and 0.23, p <

415 0.0001 respectively). Similarly, mean sediment coarseness (D50) and mud content was also

416 directly correlated with polychaetes (PC2, 0.38, p < 0.0001, 0.30, p < 0.0001). Indirect effects

417 of environmental variables were also observed on assemblage compositions: temperature had

418 indirect effects on bivalves (PC1, β= -0.15, p < 0.02) mediated by their effects on below-ground

419 biomass. Therefore, the indirect effect of temperature enhanced its direct effect on PC1. At the

420 local scale, diversity indices identified a different set of conditions and more cascading effects

421 of the environment mediated by eelgrass trait responses (**Fig. 6**). The Δ water level had the

422 greatest effects on richness, having positive direct effects on species richness (β= 1.00, p<

423 0.0001) and functional richness (FRic, β= 0.98, p< 0.0001). Species richness was also

424 positively correlated with temperature (β= 0.39, p< 0.02). Indirect effects of environmental

425 variables were also observed on local diversity indices: temperature, Δ water level and current

426 velocity had indirect effects on species richness abundance and FRic mediated by their effects

427 on leaf width and length. Because of these indirect effects on species richness, the direct

428 positive effect of temperature and Δ water level was attenuated. Abundance and richness was

429 also correlated with PC1 and PC2, showing direct positive correlation with polychaetes and

430 bivalves, respectively. Morphological characteristics of the eelgrass beds had overall weaker

431 effects on assemblage composition at regional scale than environmental variables, but had

432 greater effects on species richness abundance and FRic. All coefficients and their associated

433 p-values for the SEMs model are presented in **Table S3.2**.

Discussion

435 Eelgrass engineers highly productive habitats providing physical structure in

436 sedimentary bottoms, enhancing community diversity and biomass, as well as affecting

437 ecological key functions such as primary and secondary production (Boyé et al., 2019; Duffy,

438 2006b; Kenneth L. Heck et al., 2008). Here we examined multiple facets of biodiversity in five

439 meadows spanning ~800 km of the Atlantic coast of France in order to better understand the

440 factors that explain community diversity associated with eelgrass at different spatial scales.

Processes underlying local diversity

442 The foundation species *Z. marina* tends to have positive effects on the diversity and

443 abundance of its associated organisms (Boström et al., 2006). Data collected for the five sites

444 studied here showed that at the local scale, the number of polychaete, bivalve and gastropod

445 species, and in particular their abundances, were significantly greater in meadows when

446 compared to nearby bare sediments in nearly all sites. On average less than 15% of the

447 species were found only in the bare sediments, while more than 60% were unique to meadows.

448 Eelgrass has been shown to favor high levels of species richness and densities throughout its

449 distribution (Orth, 1977; Edgar et al., 1994; Fonseca et al., 1990; Fredriksen et al., 2010; Orth

450 et al., 1984; Stoner, 1980; Törnroos et al., 2013). This is likely due to a variety of trophic

451 resources being available in meadows, such as epiphytes on eelgrass leaves or the

452 accumulation of organic matter in meadows (Hemminga & Duarte 2000, Duffy 2006). In

453 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.,

481 2019; Kark & van Rensburg, 2006). In this study, faunal assemblages found in the core or

482 edges of the meadows did not show strong differences in richness or abundance, although the

483 cores of some meadows tended to have greater diversity or richness (but none showed both).

484 Studies that examined fine-scale differences in diversity within meadows did not identify any

485 consistent trend when comparing core and edge sectors, with most taxa showing no significant

486 edge responses. (Boström et al., 2011). However, peracarid crustaceans consistently showed

487 greater densities along edges compared to interior parts of a patch or meadow (Boström, 2006;

488 and references therein) and fish also showed higher abundance and/or richness in meadow

489 edges (Boström et al., 2011). In contrast, infaunal assemblages have generally shown no

490 significant differences in diversity when comparing habitat cores and edges (Bowden et al.,

491 2001; Tanner, 2003; Turner et al., 1999). Taxa with high mobility may respond differently to

492 habitat edges than less mobile species. In our study, polychaete, gastropod and bivalve

493 assemblages, three largely infaunal groups, showed no difference in trait composition, nor

494 proportions of mobile species at meadow edges. The absence of highly mobile species in our

495 dataset may therefore partly explain why no differences in abundance or richness were

496 detected between the core and the edges of the meadows. Infaunal communities may be less

497 affected by differences in predation pressure, predation avoidance, or other factors prevalent

498 in edges which may have stronger effects on mobile fauna (Frost et al., 1999). In sum, at the

499 local scale, community diversity and abundance were strongly favored by the presence of

500 meadows over bare sediment, but meadow modality (core or edge) did not have a strong effect

501 on the communities studied here, suggesting that ephemeral patches of eelgrass may provide

502 similar benefits to biodiversity as stable cores.

503 **Taxonomic and functional diversity at the regional scale**

504 Significant spatial variation was observed in assemblages from the five meadows

505 studied here. Taxonomic differences among sites were accompanied by changes in the

506 abundances of specific trait combinations. The Dinard meadow was rich in bivalves and

507 characterized by high abundances of small suspension feeders, the Sainte-Marguerite

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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

536 (Ouisse et al., 2012) may act as a central resource leading to the observed difference in

537 dominance of grazers, suspensory sessile microphages, or species with upward and

538 downward transport activity (Boyé et al., 2019). Here we showed the importance of considering

539 multiple components of diversity and especially β-diversity patterns to fully understand

540 meadow richness at broad spatial scales.

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

543 At local scales, parameters that describe meadow complexity (e.g. biomass, LAI, shoot

544 density) have been shown to directly influence species-level responses (e.g. growth, mortality,

545 predation, movement, reproduction; (Boyé et al., 2022; Fonseca & Bell, 1998; Koch, 2001;

546 Robbins & Bell, 2000). However, the relative importance of different biotic and abiotic factors

547 in explaining the variability and diversity of communities associated with eelgrass at the

548 regional scale has proven more difficult to understand because they typically covary (Bowden

549 et al., 2001; Hovel et al., 2002; Turner et al., 1999). Our pSEM model has helped to clarify the

550 relative contribution of certain parameters that influence community composition, as well as

551 taxonomic and functional diversity in eelgrass, as has been determined for other foundation

552 species (Lamy et al., 2020; Miller et al., 2018). The pSEM shows that differences in faunal

553 assemblages at the regional level are primarily explained by direct effects of the environment,

554 particularly by positive relationships of temperature and Δ water level on the relative

555 proportions of bivalves and gastropods. Current velocity had a significant negative direct effect

556 only on the relative proportion of bivalves, while sediment coarseness and mud content favored

557 polychaete assemblages. Temperature and Δ water level were therefore the main drivers of

558 assemblage in the meadow of Arcachon and Dinard, characterized by high abundances of

559 gastropods and bivalves respectively. Sediment coarseness and mud content were the main

560 drivers of diversity in a meadow such as Sainte-Marguerite which was rich in polychaetes or

561 Ile d'Yeu which presented species specific to certain types of sediment as the genus *Magelona*.

562 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

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

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

639   Finally, this study demonstrated that the geographic distribution of the meadows at the
640   regional scale had stronger effects of benthic community composition, with only small effects

641   of the structural characteristics of the meadows. Meadows appear to harbor subsets of species

642   observed at regional scales, and patterns of community diversity are consistent with the spatial

643   distribution of the meadows, rather than with meadow-scale dynamics. These patterns may be

644   indicative of a metacommunity system and suggest that the processes that maintain diversity

645   in meadows may reflect a seascape composed of many habitats connected by source-sink

646   dynamics. If this is the case, conservation of eelgrass systems will require a spatially diverse

647   network approach that preserves many habitats rather than considering meadows only.

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1230 DATA AVAILABILITY STATEMENT

1231   All data are available in SEANOE

1232   (https://www.seanoe.org/html/request/87709/57jfKFL2hyXopBVXNiMv/93250.zip).

1233 CONFLICT OF INTEREST

1234   The authors declare that the research was conducted in the absence of any commercial or

1235   financial relationships that could be construed as a potential conflict of interest.

1236 BIOSKETCHES

1237   Alexandre Muller is a PhD student in marine sciences at the Université de Bretagne

1238   Occidentale. He is also a member of the LEBCO team at the DYNECO laboratory at ifremer in

1239   Brest, France. His main research interests are in the macroecology of marine benthic

1240   communities, with a particular interest in the role of ecosystem engineers in the spatial

1241   variability of communities. He uses numerical ecology tools to explore the multiple facets of

1242   biodiversity and their underlying processes across spatial scales.

1243 TABLES

1244   **Table 1:** *Spatial variability of species richness, Simpson's index and abundance per m² for*

1245   *Zostera marina meadows at five sites located in metropolitan France. Mean values are*

1246   *displayed with their standard deviations. Values in bold indicate the number of species*

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

1249 **FIGURES**
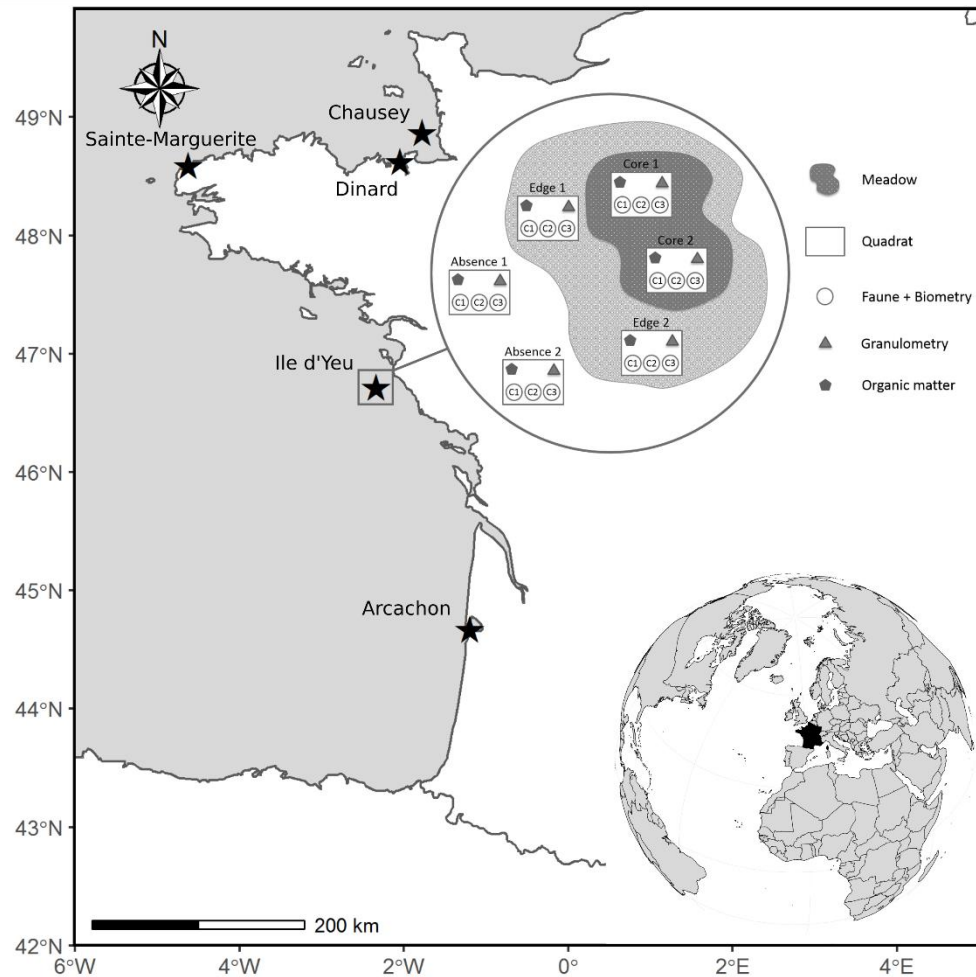
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1251 **Figure 1.** *Map indicating the locations of the 5 study sites of* Zostera marina meadows *in*

1252 *France: three in the The English Channel, and two in the Bay of Biscay. (All sites were*
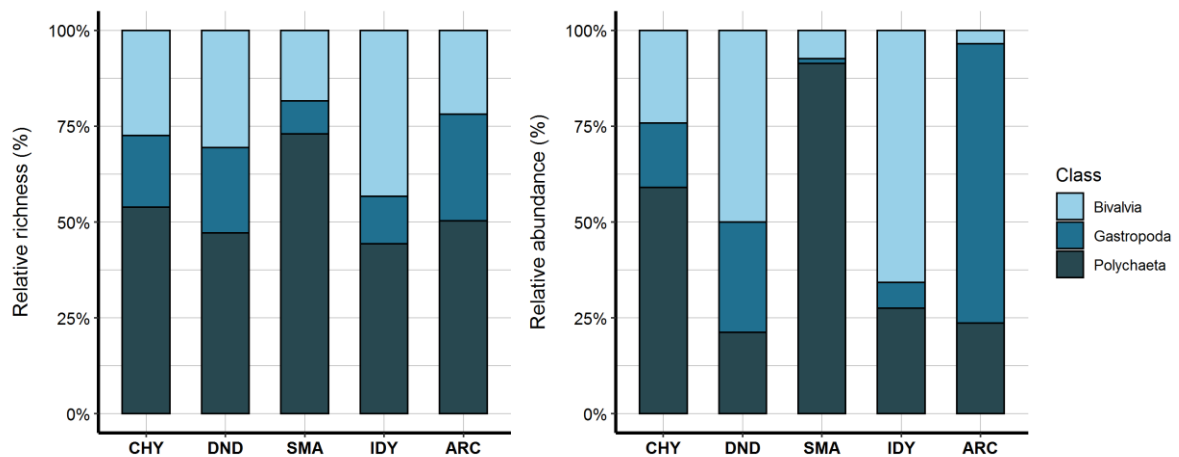
1253 *sampled in six different stations).*
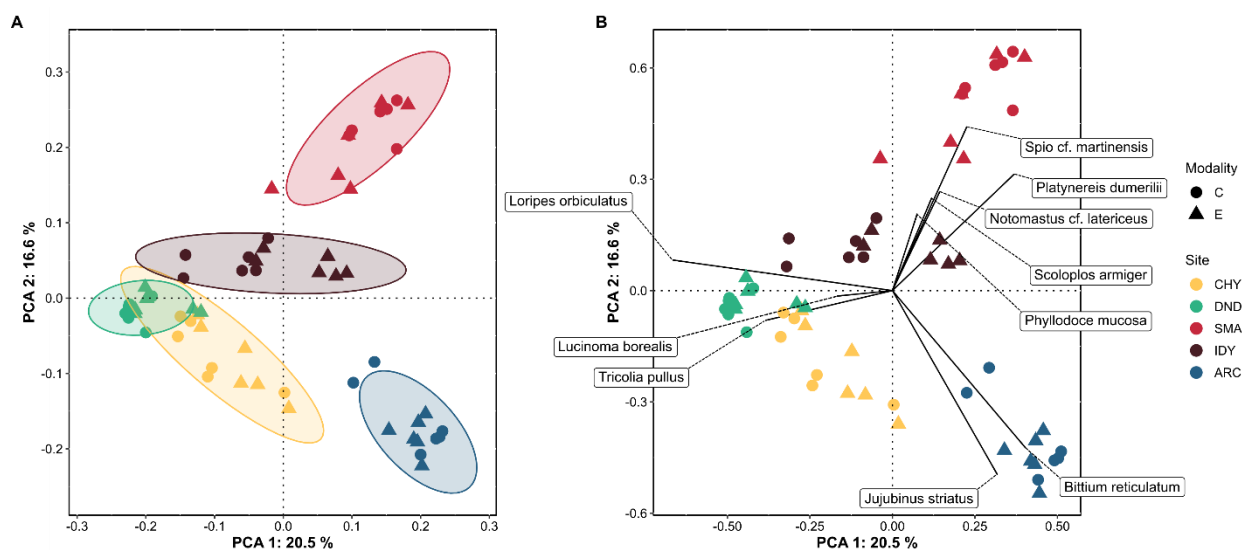
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1260   ***Figure 3.*** *Principal component analyses of the Hellinger-transformed abundances for total (A*

1261   *& B), mollusca (C & D), and polychaeta (E & F) fauna of the five Zostera marina beds sampled*

1262   *on two modalities, core and edge.* ***A.*** *the sites for each point sampled in core and edge with*

1263   *their 95% confidence dispersion ellipses, represented in scaling 1 (distance biplot) preserving*

1264   *the distances among the sites. Within-site dispersions represent variation of the communities*

1265   *among modalities.* ***B.*** *Positions of the species for which the two first axes represented at least*

1266   *40% (cumulative R2) of their variance, represented in scaling 2 (correlation biplot) preserving*

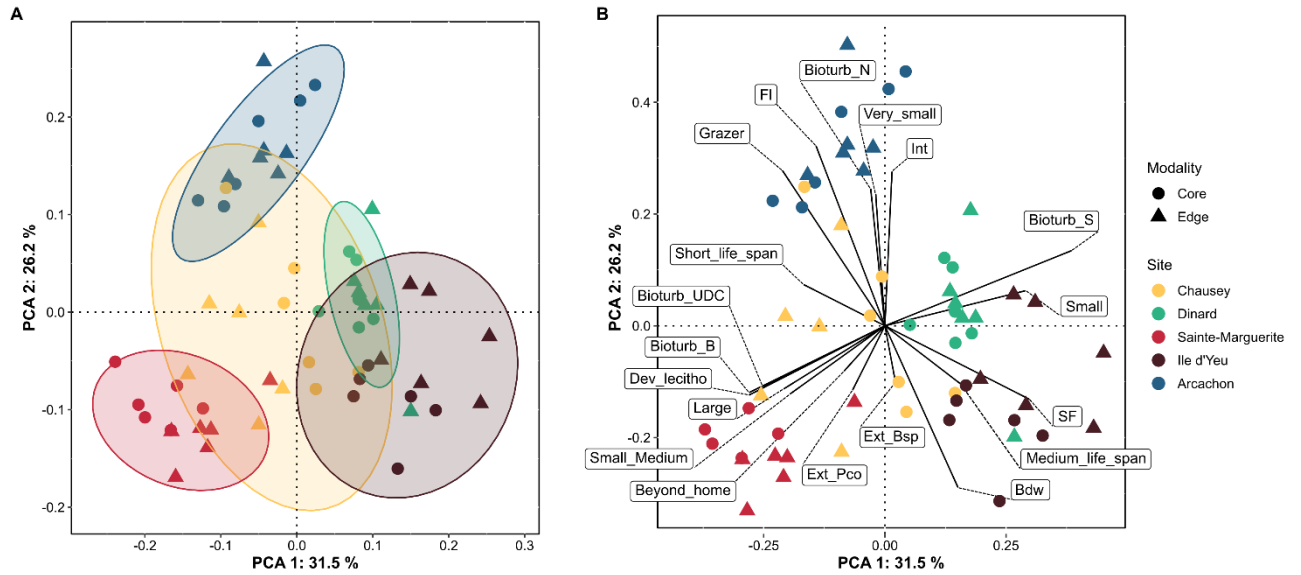1267   *the covariances among the species.*

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.*
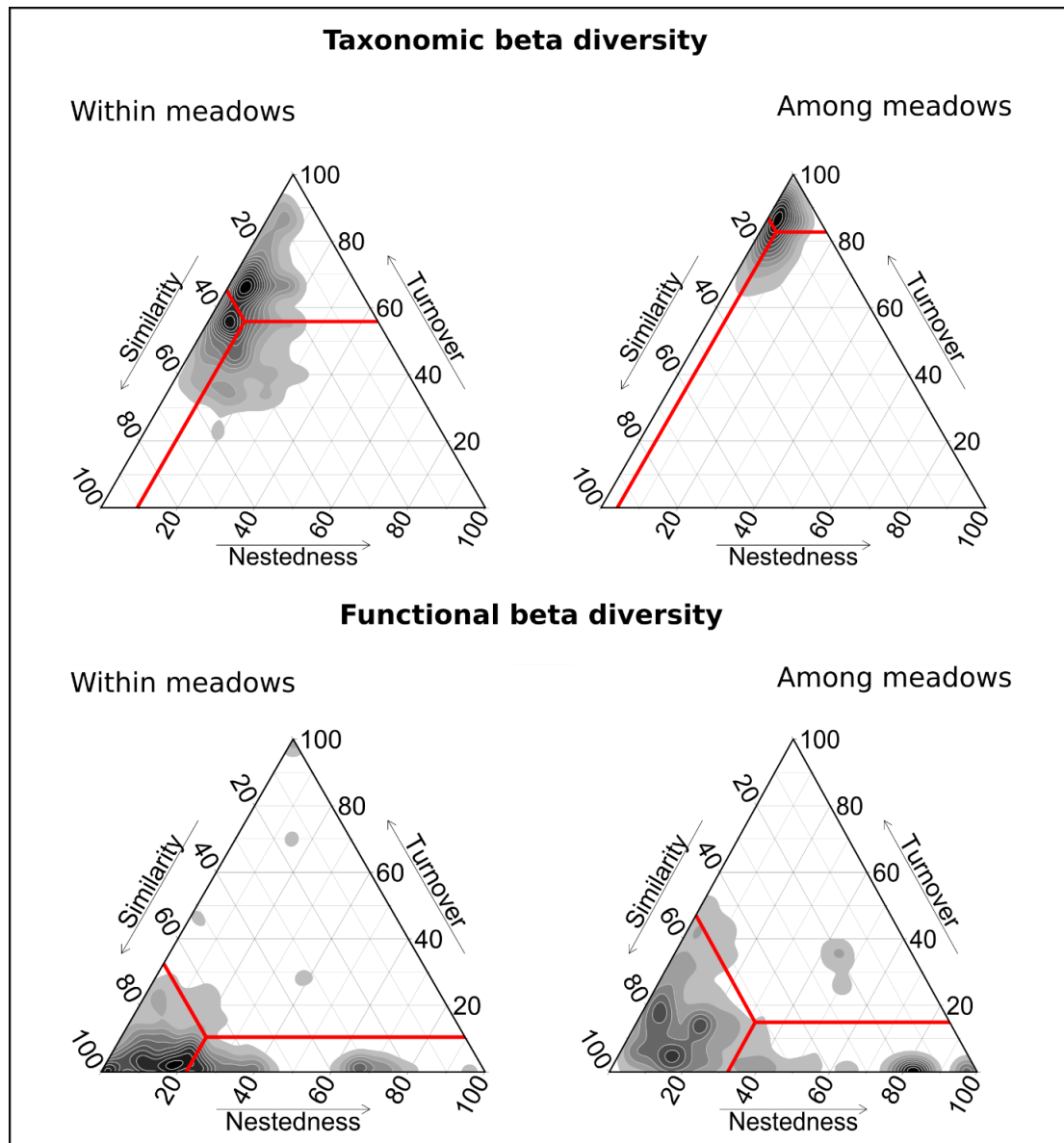
Figure 5: *Triangular plots illustrating the spatial variations of the taxonomic β-diversity. Sorensen dissimilarity between the species composition (presence/absence data) of the five seagrass beds was used to quantify their similarity, and the two components of their beta diversity nestedness (i.e. 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.*
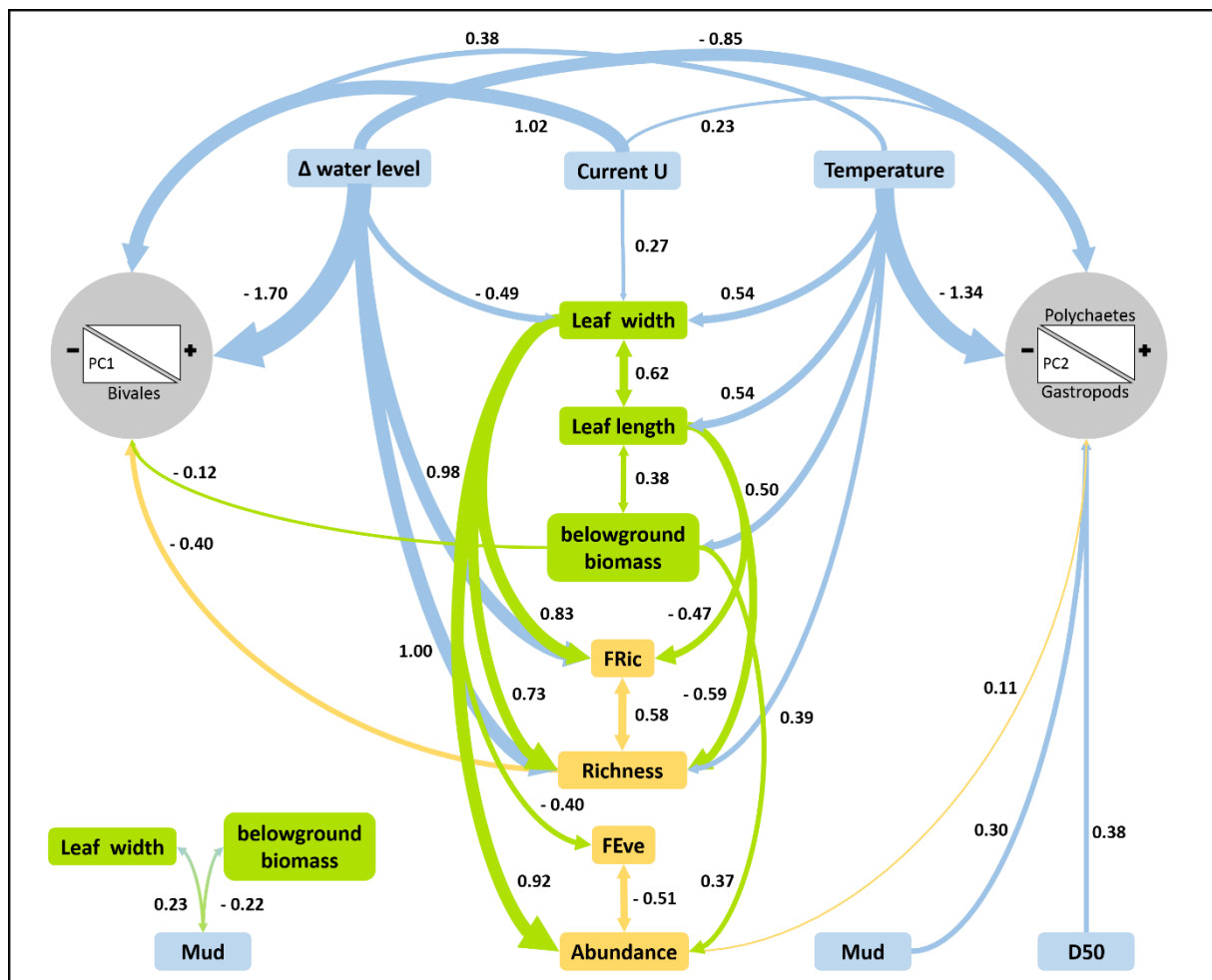
Figure 6: *Best model fitted with piecewiseSEM (structural equation modeling) describing the relationships among Zostera marina traits (in green) and environmental variables (in blue) on the principal component analyses of the Hellinger-transformed abundance (in gray). Arrows indicate directional effects. 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. R²: 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.*

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