



Eelgrass meadows harbor more macrofaunal species but bare sediments can be as functionally diverse

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ABSTRACT

Seagrass meadows are important ecosystem engineers, providing habitat for a range of marine organisms which sustain many ecosystem functions. Due to global loss of seagrass, conservation and restoration incentives are rapidly increasing. However, it is not well understood how environmental setting affects the structural and functional diversity of macrofaunal communities in eelgrass meadows (*Zostera marina*), and to what extent their importance as macrofaunal habitat is affected by abiotic variables across spatial scales. In the present study, we explored macrofaunal communities in eelgrass meadows and adjacent bare habitats across contrasting environments in Southern Sweden. We assessed taxonomic and functional diversity in concert and evaluated environmental properties as explanatory variables for the observed differences. Our results showed that eelgrass meadows supported a significantly higher taxonomic richness and abundance compared to adjacent bare sediments whereas differences in structural and functional diversity was mainly a function of site and highly influenced by dominance of the polychaete *Pygospio elegans*. Interestingly, functional redundancy was higher in brackish compared to marine sites, illustrating the effect of generalist species that cover a wide range of functional traits. Abiotic sediment variables did not explain the variation in structural or functional diversity, but were largely overshadowed by the effect of eelgrass and its belowground biomass. From a restoration perspective, our results imply that the positive effects of eelgrass restoration are similar across environments and that the presence of eelgrass is the most important factor in structuring benthic communities, but the effects on functional diversity and redundancy need further attention.

1. Introduction

Seagrass meadows sustain a plethora of ecosystem functions, which underpin the valuable ecosystem services they provide (Barbier et al., 2011; Nordlund et al., 2016). Many of these functions are due to high primary production of the seagrass and its associated epiphytes, in addition to a diverse macrofaunal community constituting an integral component of benthic secondary production (Fredette and Diaz, 1990; Heck et al., 1995). A healthy seagrass ecosystem is ultimately dependent on the taxonomic and functional diversity of its inhabiting communities and reductions in either may impair overall functioning and resilience (Sax and Gaines, 2003; Worm et al., 2006; Lefcheck et al., 2015; Pilotto et al., 2020). Due to the ongoing loss and degradation of seagrass meadows worldwide, negative impacts on marine biodiversity and ecosystem functionality are expected (Waycott et al., 2009) but the links between taxonomic and functional diversity remain elusive (Micheli and Halpern, 2005; Petchey and Gaston, 2006). It is therefore imperative to

better understand the role of seagrass meadows in structuring benthic communities across different environmental settings (Cardinale et al., 2012).

Most studies exploring benthic macrofauna in seagrass meadows have found seagrass meadows to support higher taxonomic diversity compared to adjacent bare habitats (e.g., Stoner, 1980; Edgar et al., 1994; Boström and Bonsdorff, 1997; Webster et al., 1998; Lee et al., 2001; Fredriksen et al., 2010; Möller et al., 2014), although contrasting evidence exist (e.g., Barnes, 2014; Xu et al., 2018). Yet, considerably less effort has been directed towards functional diversity, which does not always follow the same pattern despite higher taxonomic diversity in the seagrass habitat (e.g., Gross et al., 2017; Boyé et al., 2019). The general assumption that higher habitat complexity results in higher taxonomic diversity and thereby higher functional diversity is thus challenged (Dolbeth et al., 2013; Wong and Dowd, 2015), and there is a growing recognition of how spatial scale is influencing the relationship between the two (Devictor et al., 2010; Edie et al., 2018; Jarzyna and Jetz, 2018).

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Nevertheless, studies specifically relating taxonomic and functional diversity to environmental variability are scarce, especially in seagrass systems (but see, Boström et al., 2006b; Boström et al., 2010; Dolbeth et al., 2013; Wong and Dowd, 2015). Consequently, the underlying mechanisms behind different taxonomic and functional relationships are not fully understood and seem to vary depending on what spatial scales are assessed (Bremner et al., 2006; Wong and Dowd, 2015). It has been proposed that seagrass characteristics such as shoot density (Webster et al., 1998), meadow size (Eggleston et al., 1998) and seagrass biomass (Mattila et al., 1999; Lee et al., 2001) best explain differences, while other studies have isolated abiotic variables such as level of exposure (Turner et al., 1999; Boström et al., 2006b) or sediment characteristics (Frost et al., 1999; Bowden et al., 2001) as best predictors of macrofaunal community composition. On larger spatial scales, interspecific interactions among epifauna may modulate or confound the response to abiotic and biotic factors, and species-specific responses to such factors may confound the effect on community metrics such as species richness or total abundance (Whippo et al., 2018; Stark et al., 2020; Murphy et al., 2021). Understanding what is driving spatial variability in taxonomic and functional diversity is essential for predicting consequences of structural change on ecosystem functioning but also for informing coastal management interventions such as restoration, which relies on strategically selecting areas where both effective recolonization and improved ecosystem functioning and resilience can be achieved.

To address this, comparing the contribution to ecosystem functions of individual species through their functional traits can provide insight into the relationship between faunal communities and their ecosystem (Morais et al., 2019) and may serve as a qualitative proxy for ecological and biogeochemical functions (Braeckman et al., 2010; Kristensen et al., 2014). Moreover, understanding the relationship between taxonomic and functional diversity is important in the context of the redundancy hypothesis (Walker, 1992), whereby ecosystems with multiple species fulfilling similar functional roles are expected to be more resilient to natural or human perturbations (Naeem and Li, 1997). For instance, significant reductions in seagrass-associated mesograzers, as observed on the Swedish west coast, can have substantial ramifications for the ability of alleviating stressors associated with eutrophication (Jephson et al., 2008; Riera et al., 2020). Yet, the relative importance of specific species exerting important top-down or bottom-up control compared to the overall functional diversity remains elusive. As such, quantifying structural and functional diversity in tandem can be a viable tool for evaluating ecosystem functionality, but also in identifying key species and vulnerable seagrass systems.

Eelgrass (*Zostera marina* L.) is the dominating seagrass species in Sweden and grows on shallow soft bottoms from the North Sea to the Baltic Proper (Boström et al., 2014). While it is locally abundant in certain areas, a full recovery relative to historic distributions prior to the 1930s wasting disease is hampered by a suite of anthropogenic stressors (Krause-Jensen et al., 2020) and ongoing eelgrass loss is exacerbated by local regime shifts (Nyqvist et al., 2009; Moksnes et al., 2018). Therefore, large-scale restoration initiatives have developed over recent years with success rates varying with local context (Eriander et al., 2016; Moksnes et al., 2018; Nilsson and Jönsson, 2019). The overarching goal of the present study was thus to explore the expected effects on biodiversity from eelgrass restoration in different environmental conditions with the objectives to investigate (1) the macrofaunal diversity and geographical between-site differences in vegetated (*Z. marina*) and bare habitats; (2) if environmental variables can explain the composition of macrofaunal communities; and (3) how functional diversity differs between habitats and how this relates to taxonomic diversity and functional redundancy across spatial scales. To approach this, we sampled benthic macrofaunal communities in eelgrass meadows and adjacent bare habitats in five areas across a salinity gradient in Southern Sweden. In addition to conventional taxonomic diversity indices, we assessed functional diversity using a trait-based methodology and evaluated environmental properties as explanatory variables for the observed

variability.

2. Materials and methods

2.1. Study area

The southern part of the Baltic Sea is a dynamic water body with a marked salinity gradient influencing barotropic flows that are highly variable in magnitude and direction (Mattsson, 1996). Although microtidal and lacking major temporal fluctuations in salinity, the Baltic Sea can be viewed as a large estuary with river inflow and precipitation significantly exceeding evaporation rates and with a residence time of ~30 years due to its limited water exchange with the North Sea (Stigebrandt and Gustafsson, 2003; Leppäranta and Myrberg, 2009). Its only connection to the open ocean is through the Danish Belt straits and Öresund (Fig. 1), which supply saline and oxygenated water to the brackish Baltic Sea (Lintrup and Jakobsen, 1999). Due to a shallow sill this supply is limited to extreme weather events, and due to the large salinity difference between the two end members Öresund is highly vertically stratified with a strong halocline between high salinity bottom water and low salinity surface water (Lumborg, 2005; Leppäranta and Myrberg, 2009).

Field sampling was conducted in August 2019 at five sites along the coast of Southern Sweden, three on the south-west coast in Öresund (HOG, RAA, RYD), and two sites on the south-east coast in the Baltic Sea (AHU, OLA; Fig. 1). These sites are located along a salinity gradient from highly variable meso- to polyhaline conditions in Öresund (HOG, RAA, RYD) where salinity ranges from 5 to 34, to more stable oligohaline conditions on the east coast (AHU, OLA) ranging from 5 to 11 (Winsor et al., 2001; Feistel et al., 2010). The high temporal variability in Öresund is driven by alternating north- or south going surface currents which can drastically increase or decrease salinity, respectively, on short timescales (days, weeks). In contrast, the salinity at sites AHU and OLA is very stable all year around resulting in a distinctly different salinity regime as compared to Öresund.

Eelgrass meadows at each site were selected based on underwater surveys (County Administrative Board Skåne, 2016; Emanuelsson et al., 2019; Nilsson and Jönsson, 2019). These were targeted to be utilized as donor or reference meadows for a large-scale eelgrass restoration project in Southern Sweden (www.lifecoastadaptenglish.se). The eelgrass meadow at OLA has previously served as a reference meadow for an eelgrass restoration project in Kalmar county (Nilsson and Jönsson, 2019).

2.2. Sample collection

At each site, samples of benthic macrofauna, sediment properties and eelgrass morphological characteristics were collected by freediving. All samples were collected at randomly selected locations near the upper-depth limit of the eelgrass meadow (2–3 m depth), but at least 2 m from the meadow edge to avoid potential edge effects on community structure. Sediment cores for macrofauna and eelgrass belowground biomass were collected using a hand-held polycarbonate corer (inner diameter, Ø: 6.6 cm; length 30 cm). At each site, 10 cm deep cores were collected from both vegetated and bare habitats, and directly transferred into sealable plastic bags. A total of 18 cores (9 vegetated +9 bare) were collected at each site except at OLA where 12 cores (9 vegetated +3 bare) were collected and sampling depth was deeper at the bare site (~3.9 m). Bare habitat cores were taken from adjacent bare sediments ≥2 m from the *Zostera*-sand boundary except at OLA where bare samples were collected further away (Fig. 1). The uneven replication at OLA was due to logistical constraints on finding a representative bare location adjacent to the meadow. At all sites, bare patches larger than 10 m² devoid of vegetation were found, except at HOG where sparsely distributed eelgrass shoots were present in the bare habitat. To investigate spatial variability at both small (1 m²) and larger (10s of m²)

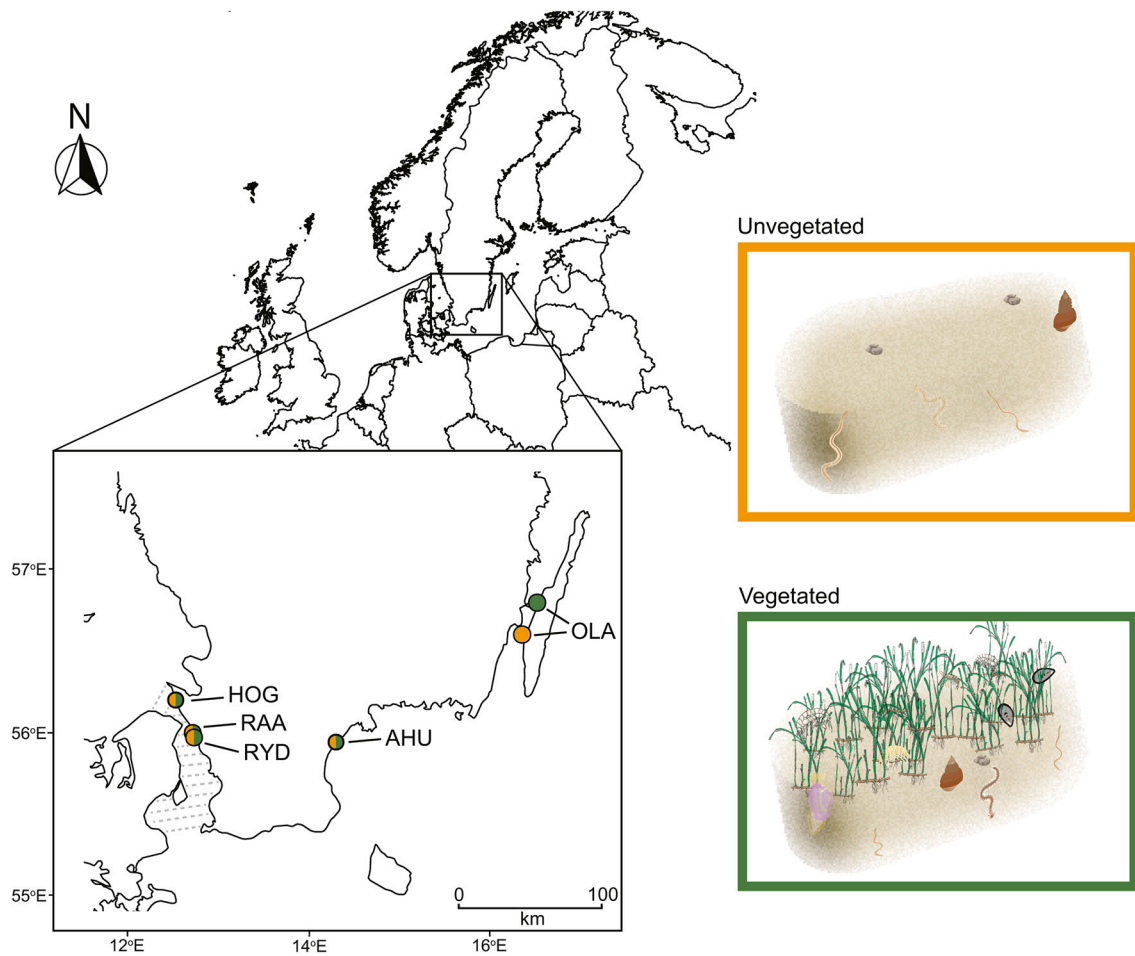


Fig. 1. Map of sampling sites HOG=Höganäs, RAA=Råå and RYD=Rydebäck, AHU=Åhus, OLA=Öland. Grey, dashed area indicates Öresund. Each site included bare (yellow) and vegetated (green) habitats except OLA where habitats were sampled in different areas. Symbols of seagrass and benthic fauna used in illustrations courtesy of the Integration and Application Network (IAN), University of Maryland Center for Environmental Science (ian.umces.edu/symbols).

spatial scales, cores were sampled in three different, randomly selected locations within the habitats, and each location was replicated ($n = 3$) in each habitat. Due to the low abundances in many bare habitats, data from each location were pooled resulting in three pooled samples per habitat per site. For analyses of sediment characteristics, smaller sediment cores (\varnothing : 5.4 cm, depth 10 cm) were collected in each location ($n = 1$ per location) and directly transferred into sealable plastic bags, except for bare sediments at OLA where no such core was collected. After sampling, bags were kept on ice in a cooler during transport back to the laboratory before being stored in a -20°C freezer. Data on annual mean salinity at each site were obtained from the Swedish Meteorological and Hydrological Institute (SMHI; www.sharkweb.smhi.se) for the five most recent years (2015–2020) whereas in situ temperature and salinity on the day of sampling was recorded using a CTD multiprobe (AAQ1183, AquaQuality).

2.3. Macrofaunal analysis

Samples were thawed in a water bath and sieved using a 0.5 mm sieve, after which macrofauna was sorted and preserved in 70% ethanol. Fauna was identified to lowest taxonomic level possible and counted using a stereomicroscope. For biomass measurements, fauna was divided into the major groups: polychaetes, bivalves, *Mytilus edulis*, gastropods and crustaceans. *M. edulis* was kept separate as their biomass overshadowed that of other bivalve species. The fauna of each core pool was combined as some pools contained too few individuals of certain

groups, which meant that their biomass was lower than the precision of the scale (0.001 g). Biomass was recorded as wet weight (WW, after being blotted on tissue paper for 1 min), dry weight (DW, 60°C for 48 h) and ash free dry weight (AFDW, after being combusted in a muffle furnace at 520°C for 4 h). Biomass of bivalves and gastropods was determined with shells.

2.4. Eelgrass characteristics

At each site, underwater photographs of each sampling location were taken to qualitatively assess morphological characteristics of the habitat (e.g., patchiness) and presence of other macrophytes (e.g., *Stuckenia* spp., *Ruppia maritima*), macroalgae (e.g., *Fucus* spp., *Chorda filum*) and filamentous algae. As macrofauna was collected from sieved samples, roots and rhizomes were simultaneously collected to determine eelgrass belowground biomass. Belowground biomass was measured as wet weight and dry weight as described above. Shoot density was measured by enclosing a frame (0.12 m^2) attached to a 1 m long nylon net bag (1 mm mesh size) over selected locations in the meadow ($n = 3$ per meadow) after which eelgrass shoots were cut off and counted. Shoot density assessments were performed in June and August 2019 whereas data collected in a previous study at OLA were obtained from Nilsson and Jönsson (2019) due to logistical constraints during sampling.

2.5. Sediment properties

Sediment samples were thawed in a room-temperature water bath and visible plant biomass, macrofauna and large stones were removed. After homogenization of the samples, a subsample (~20 mL) was extracted from each core for porosity, water content and dry bulk density (DBD) determination. Subsamples were rinsed with deionized water and transferred into 50 mL Falcon tubes. Overlying water was removed using a syringe, wet volume and wet weight was recorded after which samples were dried at 60° C until constant weight. One additional subsample (~130 g) per core was collected for analysis of grain size distribution and organic matter content and dried at 60° C for 36 h. For organic matter analysis (loss on ignition, LOI), three 5 g replicates were extracted from each subsample, homogenized using a pestle and mortar, dried at 105° C for 24 h, weighed and combusted in a muffle furnace at 520° C for 4 h. Organic matter content (OM%) was calculated as the difference in DW prior to and after combustion (Heiri et al., 2001). Samples for the bare habitat at RYD ($n = 3$) were too muddy to allow for accurate water content determination and an empirical logarithmic (ln) relationship between OM and water content from the other samples was used to estimate water content, following Moksnes et al. (2016). Similarly, the missing DBD values ($n = 5$) were estimated using the linear relationship between water content and DBD of all other samples ($R^2 = 0.91$). Grain size distribution was determined by dry sieving the remaining sediment subsample through a stack of sieves with 1 phi intervals (2, 1, 0.5, 0.25, 0.125, and 0.063 mm) with agitation for 15 min using a mechanical shaker. Each grain size fraction was weighed, after which grain size distribution, mean and median grain size (D_{50}), degree of sorting and kurtosis was obtained using the program Gradistat (Blott and Pye, 2001) in the *g2Sd* package in R.

2.6. Data analyses

All analyses were performed using R version 3.6.1 (R Core Team, 2019) and $\alpha = 0.05$ was used for statistical tests.

Ordination with Bray Curtis similarities was used to visually explore similarities between habitats by non-metric multidimensional scaling (NMDS) and was followed by a one-way analysis of similarities test (ANOSIM; Clarke, 1993).

Abundance was calculated as individuals per m^2 and species richness as number of species per pooled sample. Diversity was assessed by the Shannon-Wiener diversity index (H') and the evenness component (J'). As H' is on the logarithmic scale, it was transformed to effective numbers ($H_{eff} = \exp(H')$) to obtain linearity and scale to species richness (Jost, 2006). Data on abundance were log-transformed and biomass data were $\ln(1 + x)$ transformed to fulfill normality assumptions.

To examine the contribution of each species to the observed similarities, the similarities percentage test (SIMPER; Clarke, 1993) was used. These analyses were performed using the *vegan* package (Oksanen et al., 2019) in R. In addition, an Indicator Species Analysis was utilized to identify indicator species associated with the two habitats and the different sites (De Cáceres et al., 2010) as well as assessing the strength of association of each species to the two habitats, following the procedures in De Cáceres and Legendre (2009). Here, the presence-absence correlation index r_{ϕ}^2 (with 95% bootstrap confidence intervals) was used, which is based on Pearson correlation comparing species presence-absence in sites and site groups (i.e., vegetated or bare habitat). These two latter analyses were performed using the package *indicpecies* in R.

To assess functional diversity (FD), Rao's quadratic entropy was used (Botta-Dukát, 2005). It is one of the most applied indices for functional diversity and can be interpreted as a generalized functional analog to the Simpson diversity index (Botta-Dukát, 2005; de Bello et al., 2007). It expresses functional differences in a multivariate trait space, considering both the abundance as well as the pair-wise functional differences of species. The calculations were performed using the formula by Rao (1982):

$$FD = \sum_{ij}^S d_{ij} p_i p_j \quad (1)$$

where S is a community of species with a vector of relative abundances $p = (p_1, p_2, \dots, p_S)$, d_{ij} is the distance between species i and j calculated using Gower distance (Gower, 1966), and FD expresses the mean difference of two individuals, randomly selected with replacements and scaled by its maximum value over all frequency distributions (Botta-Dukát, 2005). Similar to H' , FD was transformed to effective numbers according to Jost (2006):

$$FD_{eff} = \frac{1}{(1 - FD)} \quad (2)$$

This puts both quantities on the same scale where the maximum value is number of species and the minimum value is 1 (Lefcheck et al., 2017). A trait-by-species matrix (Table S5) was used to construct the trait space, with species being scored a priori using fuzzy coding (Chevenet et al., 1994), following the procedure of Morais et al. (2019). Each taxon was given a score ranging between 0 and 3 reflecting association to biological trait categories, with 0 representing no association and 3 total association. Fuzzy coding enables intermediate scoring when species are associated to several functional categories, with the sum of all categories of a trait always being 3. This was done to prevent a disproportionately large influence of generalist species who fill several categories.

The trait-by-species matrix considered functional feeding group, bioturbation type, body design, movement type, and living habitat. In conjunction with calculating FD_{eff} , a posteriori number of functional groups (FGR) and indices of functional richness ($FRic$) and functional evenness ($FEve$) were computed using the *dbFD* function of the *FD* package (Laliberté and Legendre, 2010) in R. FGR was obtained by visual inspection of the functional dendrogram whereas $FRic$ expresses how much functional space is filled by each community and is thus a measure of the amount of niche space each species occupies. $FEve$ describes how evenly distributed the abundances are in the functional space and is based on the regularity with which it is filled by species (Mason et al., 2005; Villéger et al., 2008). $FRic$ and $FEve$ were included because they are independent of abundances and species richness, respectively, as opposed to FD which can be sensitive to species counts if more species with similar traits are added to a community (Villéger et al., 2008). Taxa and their functional traits were classified using literature (Bonsdorff and Pearson, 1999; Österling and Pihl, 2001; Boström et al., 2006a; Queirós et al., 2013; Breine et al., 2018), the online database World Register of Marine Species (WorMS, 2020) and the Biological Traits Information Catalogue (MarLIN, 2020). Where no information was available for a species, traits of the closest available relative within the same genus were used whereas unidentified species were excluded from the calculations.

To assess functional redundancy, the ratio between functional and taxonomic diversity (FD_{eff}/H_{eff}) was calculated, where a lower ratio implies higher functional redundancy and vice versa (van der Linden et al., 2012). In addition, linear regression analyses of taxonomic diversity (expressed as species richness or H_{eff}) and FD_{eff} was evaluated to explore habitat- or site-specific differences in their relationship (Micheli and Halpern, 2005; Petchey and Gaston, 2006).

To evaluate predictors of macrofaunal taxonomic and functional diversity, we employed linear mixed effects modelling using the *lmer* function in the *lme4* package in R (Bates et al., 2015). Models were created for each of the response variables abundance, species richness, biomass, H_{eff} , J' , FD_{eff} and its components $FRic$ and $FEve$. Habitat (bare or vegetated) and abiotic variables were selected as fixed effects whereas site was included as a random effect. The interaction between habitat and salinity was included to explore if the habitat effect on macrofauna changed along the salinity gradient. Best fit models for each response variable were chosen using forward selection based on second-order

Akaike Information Criterion (AICc; Table S1), which corrects for small sample sizes (Hurvich and Tsai, 1989). Maximum likelihood (ML) was used during model selection and once the best fit model was chosen it was refitted using Restricted Maximum Likelihood (REML) to better constrain the effects of the random factor. Assumptions of selected models were assessed for normality of residuals, homoscedasticity and autocorrelation using the *performance* package in R (Lüdtke et al., 2020). Continuous predictors were standardized to Z-scores ($Z = (x - \mu)/\sigma$) to allow for easier comparison between predictors and to reduce multicollinearity. Absence of multicollinearity of predictor variables was verified using variance inflation factors ($VIF < 2$). Type III ANOVA were used for significance testing of fixed effects using Satterthwaite's method and the random effect (Site) was tested using likelihood ratio test (LRT) where models were compared with and without the random effect included. These tests were performed using the *lmerTest* package in R (Kuznetsova et al., 2017). In the case that the random factor *Site* explained a large proportion of the variance, a separate ANOVA with only the response variable and site was run and Tukey's post hoc test (package *emmeans*) was used to test the difference between individual sites. Lastly, models were re-run on the bare and vegetated habitat separately in order to explore effects of biotic (eelgrass belowground biomass, shoot density) and abiotic sediment properties on faunal diversity in each habitat.

For models where more than one continuous predictor was significant, the variance explained by each predictor was decomposed by computing the partial R^2 using the package *partR2* (Stoffel et al., 2021). The method iteratively removes predictors one at a time, evaluates the change in variance and compares this to the full model, thereby obtaining how much of the variance is explained uniquely by each predictor. Confidence intervals (95%) of each partial R^2 were obtained by parametric bootstrapping with 100 iterations.

3. Results

3.1. Taxonomic diversity

In total, 4403 individuals representing 29 different taxa were recorded in this study (Table S2). Macrofaunal community composition was distinctly different between vegetated and bare habitats (ANOSIM $R = 0.49$, $p < 0.001$; Fig. 2) and between the different sites ($R = 0.26$, $p = 0.002$) with respect to taxonomy. A total of 25 functional traits were selected and the composition of these were significantly different between sites ($R = 0.30$, $p < 0.001$) but not habitat ($R = 0.09$, $p = 0.06$; Fig. 2).

Model selection procedures generally favored simple models with few predictors, where habitat and salinity as fixed effects generally performed the best (Table S1). Selected models revealed that that eelgrass had a relatively more positive effect on abundance at lower salinity, as indicated by the significant interaction between habitat and salinity ($\beta = -0.22 \pm 0.08$, $p = 0.02$; Fig. 3A; Table 1) whereas species richness was always higher in vegetated compared to bare habitats ($\beta = 4.95 \pm 0.70$, $p < 0.001$; Fig. 3B; Table 1). The highest number of species was found at RAA ($n = 20$), followed by RYD ($n = 17$) and HOG ($n = 16$, Table S2). On average (mean \pm SD), about twice as many species were recorded in vegetated habitats (10.9 ± 1.7) compared to bare (6.2 ± 2.1) across the entire study area. There was also a significant positive effect of salinity on abundance ($\beta = 0.32 \pm 0.09$, $p < 0.02$), with the highest abundance at the most saline site HOG ($n = 1477$) and the lowest at the least saline site OLA ($n = 471$; Fig. 3A). Faunal biomass showed a slightly different pattern between sites but was always significantly higher in vegetated habitats compared to bare ($\beta = 0.43 \pm 0.04$, $p < 0.001$; Fig. 3C) and more so with lower salinity, as indicated by a significantly negative interaction ($\beta = -0.15 \pm 0.04$, $p < 0.001$). In the vegetated habitat at RYD, a high number of adult *M. edulis* contributed to the markedly elevated biomass (Fig. 3C).

Shannon diversity (H_{eff}) displayed a contrasting pattern where bare and vegetated habitats did not exhibit a consistent difference and no model explained H_{eff} better than the null model. Evenness (J'), however, was significantly higher in bare compared to vegetated habitats ($\beta = -0.18 \pm 0.06$; $p = 0.007$; Fig. 3D–E). The tube-dwelling polychaete *Pygospio elegans* largely contributed to this due to its disproportionately high abundance especially in the vegetated habitat, which decreased diversity and evenness values. In fact, this species alone decreased H_{eff} in the vegetated habitat by as much as -5.12 (mean \pm SD = -0.22 ± 0.84) as compared to excluding it from calculations (Fig. S1). Correspondingly, when *P. elegans* was excluded from the dataset evenness was increased in the vegetated habitat resulting in H_{eff} being significantly higher in the vegetated habitat at all sites except AHU (Fig. S1).

Several species were exclusively found in vegetated habitats (the bivalve *M. edulis*, the gastropods *Theodoxus fluviatilis* and *Littorina littorea*, and the crustaceans *Heterotanais oerstedii*, *Carcinus maenas*, *Jaera albifrons*, *Idothea baltica* and *Amphibalanus improvisus*), whereas only two species were exclusively found in the bare habitats (the amphipod *Bathyporeia pilosa*, and the lugworm *Arenicola marina*). While SIMPER analysis revealed that *P. elegans*, *Hydrobia* sp. and *M. edulis* together contributed to $\sim 75\%$ of the differences between habitats (Table S3), the following multi-level pattern analysis identified nine species that were significantly associated with vegetated habitats and therefore not likely

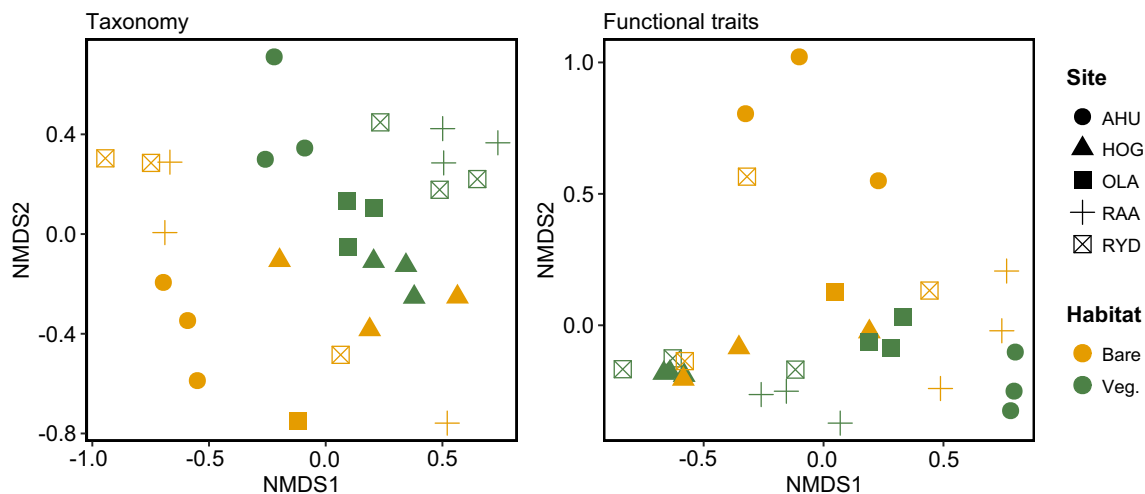


Fig. 2. Non-metric multi-dimensional scaling (NMDS) plot with Bray-Curtis dissimilarity of taxonomy (left) and functional traits (right) of benthic communities in bare and vegetated habitats. 2D stress level: 0.13 (left) and 0.08 (right) on non-transformed data.

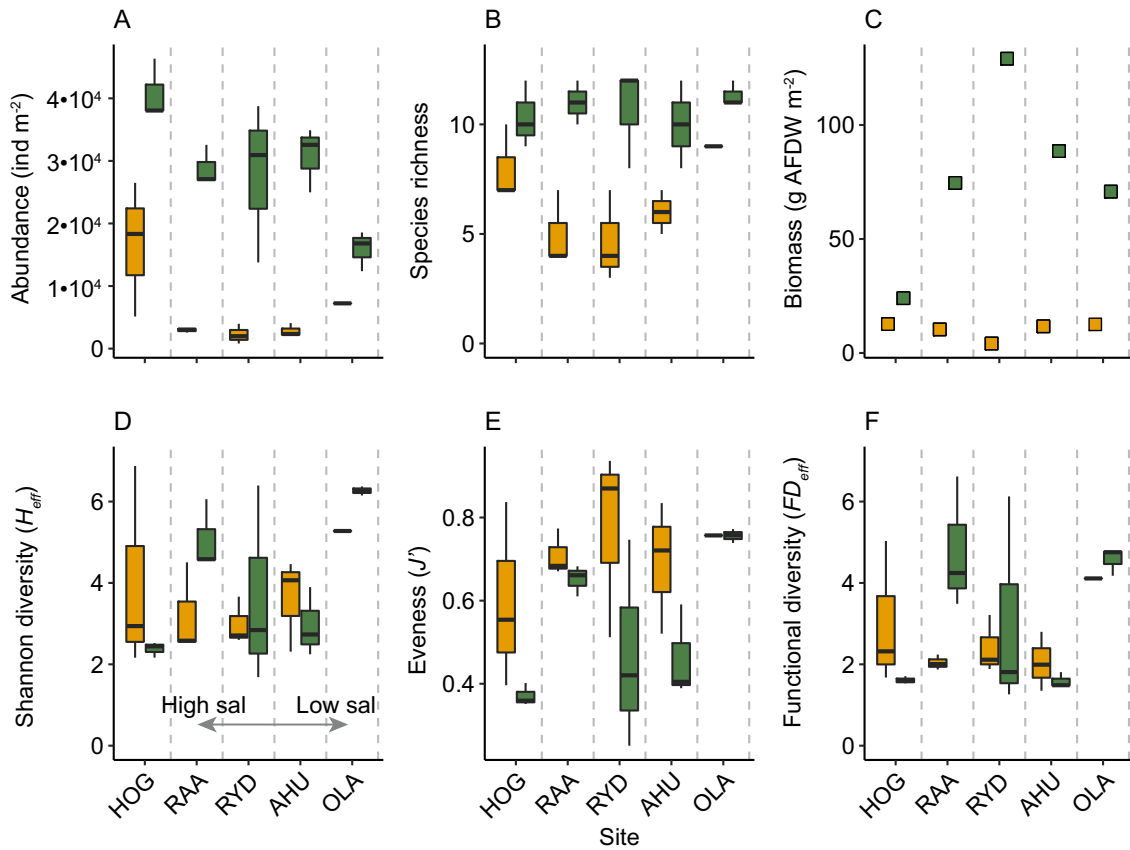


Fig. 3. Taxonomic and functional diversity in bare (yellow) and vegetated (green) habitats at the different sites. Biomass (C) represents ash-free dry weight per m² and is comprised of one pooled sample per site.

to be observed in bare habitats (Table S4). Notably, only species belonging to the functional feeding group “burrowing detritivore” displayed a stronger association with bare habitat than vegetated habitat (Fig. S2).

3.2. Functional diversity and redundancy

Patterns in functional diversity largely followed their taxonomic counterparts. Vegetated habitats comprised on average (mean \pm SD) 6.9 ± 1.2 functional groups compared to 4.6 ± 1.3 in bare habitats and functional richness ($FRic$) was always higher in vegetated habitats ($\beta = 0.29 \pm 0.06$, $p < 0.001$) whereas functional evenness ($FEve$) was marginally higher in bare habitats ($\beta = -0.13 \pm 0.04$, $p = 0.006$). Similarly to H_{eff} , there was no difference in FD_{eff} between habitats nor sites and no model outperformed the null model in terms of predictive power (Fig. 3E, Table 1). Local variation was however high, as illustrated by the vegetated habitat in RAA which displayed a considerably higher FD_{eff} than the bare habitat. The difference in FD_{eff} between this site and AHU was almost 2.8, which was a greater difference than between any other site or habitat. FD_{eff} was positively correlated with species richness ($t_{1,26} = 2.91$, $R^2 = 0.22$, $p = 0.007$) and H_{eff} ($t_{1,26} = 11.2$, $R^2 = 0.82$, $p < 0.001$) but this relationship deviated for site AHU where no clear relationship was observed (Fig. 4). FD_{eff} at AHU was also lower than that of other sites, although only significantly so compared to OLA (Tukey HSD: $p < 0.05$; Fig. 3E). When the two habitats were examined separately, the relationship between H_{eff} and FD_{eff} had a higher slope in the vegetated habitat compared to the bare habitat (Fig. 4A–B). Species richness displayed the same pattern where FD_{eff} was more strongly correlated in the vegetated habitat with twice as high slope compared to the bare habitat (Fig. 4C–D).

Functional redundancy was significantly different between sites ($p =$

0.04) but not habitat and was marginally higher (i.e., lower FD_{eff}/H_{eff} ratio; $\beta = 0.13 \pm 0.05$, $p = 0.06$) at the lower salinity east coast sites than on the west coast (Fig. 4E).

3.3. Explanatory variables for observed differences

Sediment variables differed between sites but there were no significant differences between vegetated and bare sediments (Table 2). All sites had low organic matter content ($< 1.5\%$), with some individual core pools at RYD and AHU exceeding this value. All sites had similar sediment composition, except RYD which had a higher mud content due to the presence of inorganic clay within some of the sampling locations (Table 2). Dry bulk density was very similar between sites, with only AHU being significantly lower than RAA. The highest belowground biomass (dry weight) was found at HOG with an average of 1.5 ± 0.1 g per core pool (Table 2). HOG was also the only site where eelgrass belowground biomass was observed in the bare habitat, which was higher than in the vegetated habitat in OLA (Table 2).

Model selection indicated that the inclusion of sediment variables generally did not improve the predictive power of the models (Table S1). However, when exploring each habitat (Veg./Bare) independently different patterns emerged and predictors influenced the faunal communities in variable ways. In the vegetated habitat, organic matter had a negative effect on abundance ($\beta = -0.12 \pm 0.03$, $p = 0.002$) and despite being a generally poor predictor explained 20% of the variation in abundance (Fig. 5). Contrarily, organic matter was positively related to FD_{eff} ($\beta = 1.52 \pm 0.27$, $p < 0.001$) and explained 19% of the variation in FD_{eff} . Eelgrass belowground biomass had a negative effect on species richness ($\beta = -1.05 \pm 0.36$, $p = 0.01$) and H_{eff} ($\beta = -1.33 \pm 0.35$, $p = 0.003$) but a weak, yet positive effect on abundance ($\beta = 0.11 \pm 0.04$, $p = 0.01$).

Table 1

Linear mixed effects model results for each of the structural and functional response variables. Parameter estimates (β) represent the standardized score of continuous predictors and the standard error (SE). Significance testing using type III ANOVA shows denominator degrees of freedom (df), t-statistic and p-values for fixed factors while p-values from likelihood ratio tests (χ^2) are shown for the random factor.

	Estimate	SE	df	t	p
Model: $\log_{10}(A) \sim \text{Habitat} * \text{Salinity} + (1 \text{Site})$					
Fixed effects					
Intercept	1.44	0.09	5.21	16.16	1.18×10^{-05}
Habitat Veg	0.93	0.08	21.42	11.37	1.53×10^{-10}
Sal	0.32	0.09	5.64	3.44	0.0153
Habitat: Salinity	-0.22	0.08	21.79	-2.54	0.0189
Random effects					
Site	0.14				0.0941
Residual	0.20				
Model: $S \sim \text{Habitat} + (1 \text{Site})$					
Fixed effects					
Intercept	5.92	0.52	25.00	11.27	2.71×10^{-11}
Habitat Veg	4.95	0.70	25.00	7.03	2.28×10^{-07}
Random effects					
Site	0.00				1
Residual	1.82				
Model: $\log(1 + \text{AFDW}) \sim \text{Habitat} * \text{Salinity} + (1 \text{Site})$					
Fixed effects					
Intercept	0.05	0.06	3.71	0.83	0.4543
Habitat Veg	0.43	0.04	20.54	12.01	9.54×10^{-11}
Salinity	0.04	0.06	3.94	0.79	0.4739
Habitat: Salinity	-0.15	0.04	20.77	-4.10	0.0005
Random effects					
Site	0.11				0.0089
Residual	0.09				
Model: $H_{\text{eff}} \sim 1$					
Fixed effects					
Intercept	3.79	0.31	26.00	12.16	3.12×10^{-12}
Model: $J \sim \text{Habitat} * \text{Sal}$					
Fixed effects					
Intercept	0.72	0.07	5.80	10.96	4.30×10^{-05}
Habitat Veg	-0.18	0.06	21.82	-3.03	0.0062
Random effects					
Site	0.11				0.1232
Residual	0.15				
Model: $\text{FD}_{\text{eff}} \sim 1$					
Fixed effects					
Intercept	2.79	0.30	26.00	9.36	8.21×10^{-10}
Model: $\text{FRic} \sim \text{Habitat} + (1 \text{Site})$					
Fixed effects					
Intercept	0.53	0.05	25.00	11.18	3.24×10^{-11}
Habitat Veg	0.29	0.06	25.00	4.47	0.0001
Random effects					
Site	0				1
Residual	0.17				
Model: $\text{FEve} \sim \text{Habitat} + (1 \text{Site})$					
Fixed effects					
Intercept	0.61	0.06	5.32	9.59	0.0001
Habitat Veg	-0.13	0.04	21.70	-3.04	0.0061
Random effects					
Site	0.122				0.0010
Residual	0.104				
Model: $\text{FR} \sim \text{Habitat} + (1 \text{Site})$					
Fixed effects					
Intercept	0.70	0.05	7.53	13.24	1.74×10^{-06}
Habitat Veg	0.04	0.05	22.68	-0.73	0.47
Random effects					
Site	0.08				0.04
Residual	0.12				

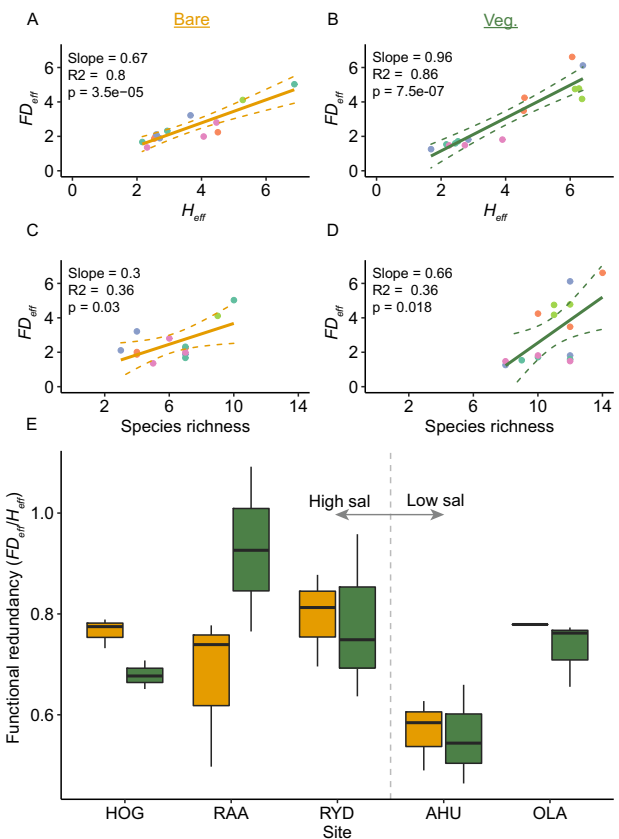


Fig. 4. Linear regression analyses of taxonomic diversity (H_{eff} and Species richness) and functional diversity (FD_{eff}) for bare (A, C) and vegetated (B, D) habitats. Point colors represent sites HOG (turquoise), RAA (orange), RYD (blue purple), AHU (pink) and OLA (green). Panel (E) shows the ratio between FD_{eff} and H_{eff} , where a lower ratio suggests higher functional redundancy. The dashed grey line separates higher salinity west coast (left) from lower salinity east coast sites (right).

4. Discussion

4.1. Structurally different but functionally similar?

Our results further underscore the importance of eelgrass meadows in structuring macrofaunal communities and indicate that this is consistent across environmental gradients. Notably, community structure varies on small spatial scales (meters) depending on vegetated status, as evidenced by the overall dissimilarity between bare and vegetated habitats (Fig. 2, Table S3). Abundance and species richness were always higher in eelgrass meadows compared to adjacent bare habitats (Fig. 3), which is in accordance with previous studies from other areas (e.g., Stoner, 1980; Edgar et al., 1994; Boström and Bonsdorff, 1997; Webster et al., 1998; Lee et al., 2001; Fredriksen et al., 2010; Möller et al., 2014; Henseler et al., 2019). While species richness was consistent throughout the salinity gradient, abundance decreased with decreasing salinity, which corroborates findings on epifaunal diversity across an estuary in British Columbia, Canada, where abundance was highest closer to the saline Pacific Ocean and gradually decreased towards the estuarine freshwater sources (Whippo et al., 2018). Notably, we observed a significant interaction between salinity and habitat and as such, the positive effects of eelgrass on community structure increased as one moved down the salinity gradient (Table 1; Fig. 3). The abundances of macrofauna recorded in this study were about an order of magnitude higher than observed in the north-eastern Baltic Proper (Möller et al., 2014) but similar to those observed in the northern Baltic Proper (Boström and Bonsdorff, 1997; Boström et al., 2002) and

Table 2

Abiotic (salinity, sediment dry bulk density (DBD), water content, mean grain size, median grain size (D_{50}) and percentage gravel, sand and mud ($<0.063 \mu\text{m}$)) and biotic variables (organic matter content (OM), eelgrass belowground biomass (BGB, dry weight) and shoot density) for the different sites and habitats (bare and vegetated). Values indicate mean \pm SD and salinity represents mean annual salinity between 2015 and 2020 for which SD represents the variability between years. n.d. = not determined.

	HOG		RAA		RYD		AHU		OLA	
	Bare	Veg.	Bare	Veg.	Bare	Veg.	Bare	Veg.	Bare	Veg.
Salinity	19.6 \pm 3.9	19.6 \pm 3.9	12.4 \pm 4.3	12.4 \pm 4.3	12.4 \pm 4.3	12.4 \pm 4.3	7.6 \pm 0.3	7.6 \pm 0.3	7.1 \pm 0.3	7.1 \pm 0.3
DBD (g cm^{-3})	1.5 \pm 0.1	1.5 \pm 0.1	1.6 \pm 0.02	1.5 \pm 0.1	–	1.6 \pm 0.1	1.5 \pm 0.04	1.4 \pm 0.01	n.d.	1.5 \pm 0.02
Water (%)	23.8 \pm 0.8	23.3 \pm 1.0	20.8 \pm 0.1	22.5 \pm 1.1	24.2 \pm 1.6	22.6 \pm 2.2	23.4 \pm 0.6	25.9 \pm 2.1	n.d.	22.6 \pm 1.1
Gr. size (μm)	169 \pm 25	171 \pm 2	280 \pm 31	248 \pm 11	201 \pm 102	207 \pm 60	186 \pm 10	184 \pm 12	n.d.	350 \pm 64
D_{50} (μm)	147 \pm 20	153 \pm 2	233 \pm 28	203 \pm 8	165 \pm 95	153 \pm 46	166 \pm 2	162 \pm 7	n.d.	232 \pm 52
Gravel (%)	–	–	0.1 \pm 0.2	0.01 \pm 0.02	0.3 \pm 0.5	1.0 \pm 1.0	–	–	n.d.	1 \pm 0.3
Sand (%)	99 \pm 1	99 \pm 1	100 \pm 0.2	100 \pm 0.1	80 \pm 21	89 \pm 14	100 \pm 0.3	99 \pm 0.3	n.d.	96 \pm 1
Mud (%)	1 \pm 1	1 \pm 1	0.04 \pm 0.01	0.2 \pm 0.04	20 \pm 21	10 \pm 15	0.3 \pm 0.1	1 \pm 0.3	n.d.	3 \pm 1
OM (%)	0.69 \pm 0.07	0.90 \pm 0.1	0.33 \pm 0.04	0.52 \pm 0.1	1.29 \pm 1.1	1.15 \pm 0.7	0.94 \pm 0.2	1.42 \pm 0.1	n.d.	0.68 \pm 0.2
BGB (g m^{-2})	88 \pm 74	175 \pm 42	–	116 \pm 32	–	134 \pm 17	–	163 \pm 14	–	81 \pm 14
Shoots (m^{-2})	–	254 \pm 69	–	167 \pm 20	–	317 \pm 43	–	398 \pm 173	–	483 \pm 132

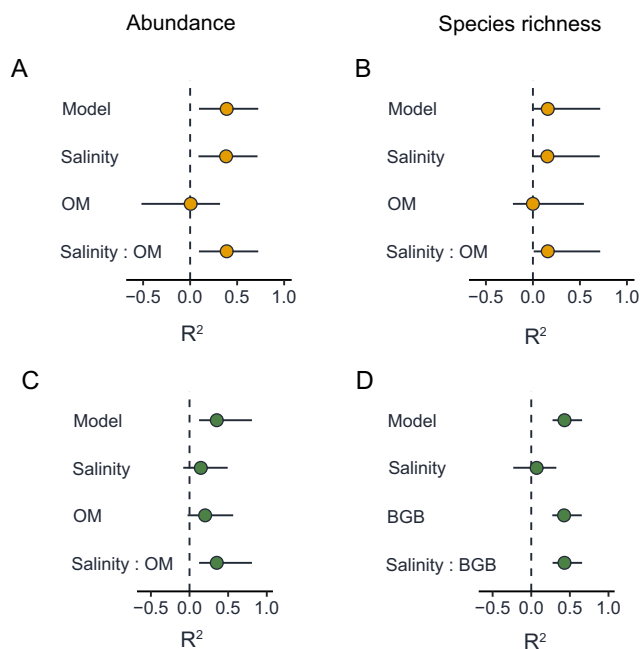


Fig. 5. Forest plots showing the semi-partial R^2 of best fit models for bare (A, B) and vegetated (C, D) habitats. Response variables are abundance (left panels) and species richness (right panels). Error bars show 95% confidence intervals and negative values are treated as null for ecological interpretations.

Skagerrak (Fredriksen et al., 2010). However, average species richness was nearly twice as high as that observed by Boström and Bonsdorff (1997) but approximately half of what Fredriksen et al. (2010) reported. As such, there is seemingly a gradient of decreasing species richness going into the Baltic Sea, that is independent of abundance. However, it should be noted that Fredriksen et al. (2010) used a finer sieve to sort fauna (0.25 mm), which likely contributed to additional species being included in their study. Clearly, differing sampling methodologies may confound comparisons between studies (Boström et al., 2006a and references therein).

Shannon diversity displayed a different pattern with no consistent effect of neither habitat nor site (Fig. 3D). Instead, the abundance of *P. elegans* largely governed differences in H_{eff} , and also contributed the most to dissimilarities between habitats (Table S3). In fact, the species' high abundance primarily in RYD and HOG vegetated habitats decreased H_{eff} by up to $\sim 70\%$. Consequently, when *P. elegans* was excluded from the calculations, H_{eff} was significantly higher in the

vegetated habitat across all sites except AHU (Fig. S1). This disproportionate influence is problematic as abundance counts of *P. elegans* are associated with uncertainty due to its fragility in sample handling and proneness to fragmentation, and thus, the abundances of *P. elegans* in this study may be slightly underestimated. Nevertheless, *P. elegans* is a common opportunistic species and is known to have a large influence on the structure of macrofaunal communities in Swedish waters in general (Olafsson and Persson, 1984; Mattila, 1997) and eelgrass meadows in particular (Boström and Bonsdorff, 1997; Boström and Bonsdorff, 2000; Kesäniemi et al., 2012). It is possible that our sampling occurred shortly after an intense reproduction period of *P. elegans* (Kube and Powilleit, 1997; Thonig et al., 2016). Reproduction occurs once or twice annually, typically in spring and autumn and population densities vary depending on environmental setting and sediment characteristics (Gudmundsson, 1985; Bolam, 2004; Thonig et al., 2016). Notably, when site RYD was revisited in early May 2020, not a single specimen of *P. elegans* was observed in samples (Carlsson, P., pers. obs), further highlighting their temporal population fluctuations. Furthermore, Kube and Powilleit (1997) proposed that *P. elegans* feeds on faeces produced by *Mytilus edulis* which exhibited the highest recorded biomass at site RYD, coincident with the second highest abundance of *P. elegans* recorded in this study. However, no such correlation between the two species was observed at HOG.

The observed differences in community structure between vegetated and bare habitats were to a large extent explained by the higher presence of epifaunal species within the former. While the core sampling technique employed in this study is targeted to sample infauna, it is evident that it also captures a wide range of small mobile epifauna. However, it is challenging to define a distinct separation between these two groups as species may migrate vertically across the sediment-water interface owing to differences in life history strategies, season and habitat characteristics and the distinction is often determined by sampling methodology (e.g., sediment cores or leaf canopy samples; Baden and Boström, 2001). We used the trait-based approach to separate in- and epifauna based on the trait categories “Movement type” and “Living habitat” (Table S5). This made it clear that epifaunal species were predominantly driving the higher taxonomic diversity in vegetated habitats, while diversity indices of infauna were largely influenced by *P. elegans*. While it is not surprising that barren sands were virtually devoid of mesograzers feeding on eelgrass epiphytes (e.g., *Gammarus* spp., *Idotea balthica*, *T. fluviatilis* (Jankowska et al., 2019)), it is noteworthy that most of these species were abundant in eelgrass and thus did not show signs of the regime shifts observed on the Swedish northwest coast where especially *Idotea* spp. and *Gammarus* spp. have diminished over the past 20 years (Riera et al., 2020).

Contrary to what we hypothesized, functional diversity as measured herein (FD_{eff}) did not exhibit a consistent difference between habitats

(Fig. 3E), with most functional trait categories represented in both vegetated and bare habitats (Table S5). The trait categories exclusive to eelgrass meadows were the bioturbation type “regenerator” and the living habitat “attached”, while the bioturbation type “surficial deposition” was exclusive to bare habitats (Table S5). As such, the higher species richness, abundance and biomass found in the vegetated habitat did not correspond to a general gain in functional diversity at the local scale but did nonetheless display a positive correlation across the whole study area (Fig. 4). Several studies have found a general positive relationship between taxonomic and functional diversity (e.g., Micheli and Halpern, 2005; Petchey and Gaston, 2006; Lefcheck et al., 2015) but this relationship is generally scale-dependent (Wong and Dowd, 2015; Bracken et al., 2017). The present study further illustrates this as the relationship between functional and taxonomic diversity was significantly positive for the entire study area, but rarely correlated at site-level (Fig. 4). Notably, this relationship was also different between habitats, where a much higher slope was observed in the vegetated habitat compared to the bare habitat (Fig. 4). Micheli and Halpern (2005) suggested an asymptotic relationship in which functional diversity increases at intermediate taxonomic diversity and plateaus at higher levels, which could here be represented by the bare habitats with less niche overlap compared to vegetated habitats (Díaz and Cabido, 2001). Again, the influence of *P. elegans* largely affected this and its high abundance in primarily vegetated habitats had a disproportionate influence on functional evenness and FD_{eff} as we based abundances on non-transformed individual counts (Petchey and Gaston, 2006; de Bello et al., 2007; Fig. S1). Based on our findings, the eelgrass macrofaunal communities remain species- and functionally rich despite its high presence, but whether this opportunistic species has any substantial effect on overall eelgrass ecosystem functioning should be a focal point in future studies.

Quantification of functional redundancy is complex and several different approaches have been employed in the literature, with the shared feature that they relate functional and taxonomic diversity in one way or another (Ricotta et al., 2016). In the present study, we used two different methods to assess functional redundancy namely the ratio between FD and H proposed by van der Linden et al. (2012) in conjunction with linear regression analyses of taxonomic and functional diversity (Micheli and Halpern, 2005; Wong and Dowd, 2015). Due to the transformation to true diversities, the ratio FD_{eff}/H_{eff} is straightforward to interpret as both the numerator and denominator are on the same scale and measured in units of number of species. As pointed out by Micheli and Halpern (2005), a strong positive linear relationship between the two implies that functional diversity is sensitive to species loss and is thus less functionally redundant. This agrees with our assessment of the FD_{eff}/H_{eff} ratio, which showed that the site with lowest ratio (AHU) deviated from this relationship (Fig. 4) and thus comprised the highest functional redundancy. This reflects how a low number of functional traits that are covered by a relatively high number of species appears to increase the biological insurance effect of the current stable state (c.f. Naeem and Li, 1997). As such, the low FD_{eff} and homogenous community at AHU can be interpreted as an indicator of environmental disturbance (Micheli and Halpern, 2005), where functional redundancy increases as perturbations result in loss of species with rare trait-categories (Wong and Dowd, 2015). This filtering of traits can eventually lead to a community of species with less unique traits and the overall decrease in trait dissimilarities renders a higher functional redundancy (van der Linden et al., 2016). The low FD_{eff} of AHU may, in part, be due to the few species of crustaceans present which are a functionally diverse group with a wide range of feeding strategies (predators, grazers, detritivores and omnivores), and movement types (swimming, crawling and burrowing). Consequently, AHU could be showing symptoms of what has been observed on the Swedish west coast, where crustacean mesograzers have drastically diminished from eelgrass meadows due to the combined effects of overfishing and eutrophication (Moksnes et al., 2008; Riera et al., 2020). However, interpreting functional redundancy

based on traits as a canary of environmental perturbations is complicated due to the fact that it can remain essentially unchanged in the event that species with similar traits are concomitantly lost (Ramsay et al., 1998; Taupp and Wetzel, 2019).

Local variability notwithstanding, there seems to be a trend of increasing functional redundancy with decreasing salinity, at least in vegetated habitats (Fig. 4). Similar observations have been made in the Western Baltic Sea, where redundancy was lowest in the area with highest salinities (21.76 ± 0.54) and highest in brackish waters (7.66 ± 0.15) (Darr et al., 2014). The authors suggested that while communities in fully marine areas are characterized by specialist species, the necessity of brackish species to cope with low salinities lead to communities with generalist species that cover a wide range of functional traits. Similarly, a reduced species diversity in brackish waters enables an expansion of niche breadth of originally marine species, which acquire a more generalist behavior (Dahl, 1973; Baden and Boström, 2001). Therefore, despite a lower number of species, functional redundancy remains high as most functional trait categories are represented by most species. Similar findings were made in an estuary in Portugal during winter, where the FD/H ratio decreased as one moved further up the river and salinity decreased (van der Linden et al., 2012). Our dataset was mostly comprised of species with marine origin which exhibited no distinct preference for either coast. The few species of limnic origin (*T. fluviatilis*, *Hydrobia* sp., *Chironomidae* sp.) all showed a higher affinity for the oligohaline east coast (Fig. S2). It is important to note that we used annual mean salinity values in this study but the intraannual variability in salinity is distinctly different between west and east coast sites (Fig. S3). The importance of highly variable compared to stable salinity in structuring benthic communities in this area should be studied further.

While assessments of trait-based functional diversity and redundancy are useful, it is important to remember that they do not translate into the ability to maintain any specific process (Pillar et al., 2013), but should rather be regarded as a means of directing future research needs in quantifying ecosystem functions. Impairment of taxonomic diversity does not necessarily render loss of functional diversity (Edie et al., 2018), and redundancy may be less important for ecosystem functions than the presence of specific species with important traits (Norling et al., 2007; Gammal et al., 2018). Moreover, an inherent limitation of comparing trait-based functional diversity between studies is that it is largely dependent on which traits are chosen and how these are characterized within the analyses (Naeem and Wright, 2003; Micheli and Halpern, 2005; Petchey and Gaston, 2006). In the present study we employed a wide approach to cover several types of interactions. Bioturbation was included due to its effect on oxygenation and biogeochemistry of sediments (Braeckman et al., 2010; Ekeröth et al., 2016), functional feeding groups were included to cover biotic interactions such as predation and herbivory but also due to its effect on nutrient cycling and benthic-pelagic coupling (Newell, 2004; Norling et al., 2007), whereas remaining traits were more general and descriptive (Table S5). This allowed for a more general measure of overall diversity, with the caveat that it prevented disentangling individual functions inferred from specific traits. The macrofaunal FD and FD_{eff} values observed in this study are in the same range as those observed in comparable seagrass meadows using the same approach (Wong and Dowd, 2015; Lefcheck et al., 2017) and across an estuarine salinity gradient (van der Linden et al., 2012). Nonetheless, the inclusion or exclusion of traits could have produced a different result and the dependence of functional redundancy on the number of traits included makes it a somewhat subjective measure (Petchey and Gaston, 2006). Further studies should therefore compare bare and vegetated habitats in terms of individual traits and relate these to quantitative assessments of specific ecosystem functions such as biotic interactions and biogeochemical processes. The division of taxa into functional groups is additionally problematic as many organisms may modify their functional traits, such as altering feeding mode due to food availability or changing

bioturbation type across life stages (Padilla and Savedo, 2013). This plasticity introduces uncertainty in deriving the contribution of species to ecosystem function, with species possibly playing different roles in different systems. Another property of FD is that it is based on abundances, meaning that species richness is not taken into consideration. An effect of this is that, under certain conditions, FD may actually decrease as species richness increases, since the mean distance in the trait-space between species may become smaller (Botta-Dukát, 2005; Laliberté and Legendre, 2010). This renders difficulties in making predictions of the effects of species loss on ecosystem functioning, if loss of an abundant but less functionally unique species will increase FD (Petchey and Gaston, 2006).

4.2. Explanatory variables for the observed differences

Many studies have tried to elucidate the drivers of macrofaunal diversity in eelgrass meadows, with largely equivocal results variable in time and space (e.g., Eggleston et al., 1998; Webster et al., 1998; Frost et al., 1999; Mattila et al., 1999; Turner et al., 1999; Bowden et al., 2001; Lee et al., 2001; Boström et al., 2006b). According to our linear mixed effects modelling, abiotic sediment variables did not explain variation in response variables, with habitat completely overshadowing the effect of sediment variables (Murphy et al., 2021). Furthermore, we found no evidence of indirect influence of eelgrass on sediment characteristics, inferred from the generally insignificant differences between vegetated and bare habitats (Table 2). Yet, organic matter content was significantly higher in vegetated sediments than adjacent bare in all sites except RYD and OLA (Table 2). At RYD, sediment composition was highly heterogeneous, in part due to the presence of patches of glacial clay in the bare sediments (Lagerlund and Houmark-Nielsen, 1993). This may explain the relatively large difference in sediment characteristics between RYD and RAA – two locations in close proximity of each other (<5 km) with similar hydrodynamic regime – and further highlights the spatial variability in eelgrass sediment properties (Kindeberg et al., 2018). Nonetheless, this heterogeneity did not translate into any significant differences in taxonomic or functional diversity in the bare sediments, but a much higher H_{eff} and FD_{eff} in the vegetated sediments (Fig. 3). It is plausible that the sites investigated in this study do not cover a sufficiently broad range in sediment characteristics to allow for its effects on macrofaunal diversity to be discerned (Gammal et al., 2018). All sites are relatively exposed from a hydrodynamic perspective, with spatiotemporally fluctuating sediment accretion and erosion (Lumborg, 2005). Consequently, the effect of eelgrass meadows on sediment characteristics in highly hydrodynamic environments could be less pronounced than in sheltered environments, and also vary depending on meadow characteristics (Bouma et al., 2005; Bos et al., 2007; Hasegawa et al., 2008; Koch et al., 2009).

However, when reexamining the two habitats separately, the R^2 partitioning indicated that biotic and abiotic predictor variables explained considerably more of the variation (Fig. 5). Despite a rather low variability of organic matter it explained 20%, and together with salinity about 36%, of the variation in abundance in eelgrass habitats (Fig. 5C). Notably, eelgrass belowground biomass was negatively correlated with species richness and H_{eff} while being positively correlated with abundance in eelgrass habitats. This was to some extent driven by *P. elegans*, which increased in abundance with increasing belowground biomass ($R^2 = 0.43$; $p < 0.001$) and thus negatively affected H_{eff} . The effect of eelgrass belowground biomass is equivocal in the literature with evidence of both positive and negative effects on abundance and species richness (Orth et al., 1984). The dichotomous effects have been attributed to both predation protection and prevention of certain hard-bodied taxa to burrow and may thus affect contrasting communities differently (Orth, 1977; Stoner, 1980; Orth et al., 1984; Lee et al., 2001). This suggests that the small-scale variability in macrofaunal diversity is primarily driven by direct effects of the eelgrass habitat, such as the three-dimensional complexity and stabilizing effects

on sediments (Boström and Bonsdorff, 1997; Gustafsson and Boström, 2011; Namba and Nakaoka, 2018; Murphy et al., 2021). Furthermore, radial oxygen release (ROL) from eelgrass roots may locally alleviate anoxia and sulfate reduction and thereby create favorable conditions for infauna (Sand-Jensen et al., 1982; Borum et al., 2007).

5. Conclusion

Collectively, our results further highlight the importance of eelgrass meadows as a habitat for macrofauna and show that this is consistent across environmental settings. The mere presence of eelgrass, rather than any specific attribute, renders highly abundant and species-rich benthic communities. Contrastingly, functional diversity and redundancy can remain high even in the absence of vegetation, likely due to the comparatively high species richness compared to trait richness and illustrates how taxonomic and functional diversity can be spatially decoupled. The marked effect of the dominant species *P. elegans* illustrates how otherwise functionally diverse eelgrass meadows can be affected by a single generalist species, but how this translates to specific functions needs further attention. Jointly, our findings can inform coastal managers in selecting areas for restoration, where taxonomic and functional measures should be used in tandem to target rare and sensitive species and for restoring overall ecosystem functionality.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2022.151777>.

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