

Patterns in Taxonomic and Functional Diversity of Macrobenthic Invertebrates Across Seagrass Habitats: a Case Study in Atlantic Canada

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Abstract Functional diversity (*FD*) characterizes the role of species within communities based on their morphological, behavioural and life history traits. Taxonomic diversity is not always a surrogate for *FD*, and ecosystem functioning is more dependent on functional traits rather than species richness. Despite this, most diversity studies in seagrass ecosystems do not consider the functional trait landscape. Here, we compare and contrast the taxonomic and functional diversity and composition of macrobenthic invertebrates (infauna and small epifauna) across a gradient of seagrass habitats (bare sediment, bed edge and bed interior) at three sites in Nova Scotia, Canada. We also determine the relationship between taxonomic diversity and *FD* to gain insight into the consequences of species loss. At two sites, we found that taxonomic diversity (species number and Margalef and Simpson's indices) increased from bare sediments to the bed interior, while *FD* (Rao index) did not or else showed a weaker pattern. At a third site, both taxonomic and functional diversity tended to increase across the seagrass gradient. Despite the differences in relationships between taxonomic and functional diversity, functional trait composition tended to be distinct across seagrass habitats at all sites. Regressions showed that *FD*

increased either hyperbolically or linearly with taxonomic diversity. Our study suggests that for seagrass ecosystems similar to the ones sampled, the implications of species loss for ecosystem functioning may not be easily predicted from data of taxonomic diversity alone. This study provides some of the first data of taxonomic and functional diversity in seagrass ecosystems, which can be used to inform conservation objectives and management practices.

Keywords Biological traits analysis · Coastal marine ecosystems · Ecosystem functioning · Rao quadratic entropy index · *Zostera marina*

Introduction

Seagrass beds are highly valued for the multiple ecosystem services they provide, including coastal protection and erosion control, carbon sequestration, maintenance of fisheries, water purification and the provision of raw materials and food (Barbier et al. 2011). Many of these ecosystem services are derived in part from functions performed by assemblages of macrobenthic invertebrates. Because benthic assemblages are influenced by plant and sediment properties (John et al. 1992; Snelgrove and Butman 1994), the degradation and loss of seagrass habitats may have important consequences for invertebrate communities and the functions they provide. The potential for such changes have become an increasingly important issue due to loss of global seagrass coverage (Waycott et al. 2009). Studies of taxonomic diversity can provide insight into the consequences of habitat change for ecosystem functioning, particularly if species' functional traits are examined (Hooper et al. 2005; Lavorel et al. 2011). Functional characteristics of species are known to strongly influence ecosystem properties and as such provide an important link

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between taxonomic diversity and ecosystem functioning (Díaz and Cabido 2001; Braeckman et al. 2010; Bolam and Eggleton 2014). While many studies in seagrass ecosystems have examined taxonomic diversity of macrobenthic invertebrates, few have examined functional trait diversity and how it relates to seagrass bed structure (e.g. shoot density and location within the bed). Knowledge of both taxonomic and functional diversity across seagrass landscapes is essential for understanding potential future change in provision of ecosystem services and to inform conservation objectives and management practices.

Several patterns are evident when taxonomic properties of macrobenthic invertebrate communities are examined across seagrass bed structure. Typically, taxonomic diversity and richness are higher in seagrass beds compared to bare sediments (e.g. Edgar 1990; Heck et al. 1995). Assemblage composition often differs in seagrass relative to bare sediments (e.g. Bologna 2006; Dolbeth et al. 2013), while composition within seagrass beds is influenced by patch size, fragmentation, location within the bed and landscape variables such as fetch and shore angle (e.g. Bowden et al. 2001; Bologna 2006; Boström et al. 2006; Mills and Berkenbusch 2009). Furthermore, abundance, biomass and secondary production of macrobenthic invertebrate communities are usually highest in seagrass beds compared to bare sediments (e.g. Edgar 1990; Heck et al. 1995; Dolbeth et al. 2003; Bologna 2006; Wong et al. 2011) but can be influenced by position within the seagrass bed (i.e. edge vs. interior; Bologna 2006).

Despite the plethora of studies that examine relationships between macrobenthic invertebrate assemblages and seagrass bed structure, relatively few have examined these relationships in terms of functional trait diversity or composition (although, see Boström et al. 2006; Boström et al. 2010; Dolbeth et al. 2013). That is, we know a great deal about how seagrass habitat structure affects species presence and abundance but lack knowledge of the functional trait landscape and how it links to ecosystem functioning. Although taxonomic diversity is often assumed to directly reflect functional diversity, this relationship is dependent on the composition of functional traits within the community, the degree of functional redundancy present, the amount of aggregation within niche space, the abundance of species relative to traits and the index used to represent functional diversity (Díaz and Cabido 2001; Micheli and Halpern 2005; Petchey and Gaston 2006; Petchey et al. 2007). The relationship between functional and taxonomic diversity can be of various forms, including an increasing linear relationship (with varying slopes possible), a saturation relationship wherein functional diversity increases at a decreasing rate to plateau at high taxonomic diversity, or even a negative relationship where functional diversity increases with decreasing taxonomic diversity (Díaz and Cabido 2001; Micheli and Halpern 2005; Petchey and Gaston 2006). Taxonomic diversity is not always a direct surrogate for functional

diversity; hence, determining the relationship between taxonomic and functional diversity is a key element for predicting the consequences of species changes or loss on ecosystem functioning. Here, we use data of macrobenthic invertebrates (infauna and small epifauna) from seagrass ecosystems in Atlantic Canada to examine this relationship.

Several approaches can be used to characterize functional trait composition and diversity across communities. Biological traits analysis (BTA) describes functional trait composition by simultaneously including multiple species traits related to life history, morphology and behaviour within ordinations (Bremner et al. 2006). BTA has been well applied to marine benthic assemblages to examine the effects of spatial and temporal scale (e.g. Bremner et al. 2006), perturbations such as trawling, dredging and eutrophication (e.g. Tillin et al. 2006; Paganelli et al. 2012; Wan Hussin et al. 2012) and implemented management measures (Verissimo et al. 2012; Dolbeth et al. 2013) on functional trait composition. While BTA is most useful to understand functional trait composition and ecosystem functioning across environmental or stress gradients, overall functional diversity can be described by a variety of indices (Schleuter et al. 2010). These indices provide insight into the nature of the functional niche space, including how much of the space is filled by existing species and the distribution of traits within that space (Lepš et al. 2006; Schleuter et al. 2010). Functional diversity indices were developed in terrestrial ecology and are well used there (Mason et al. 2005; Petchey and Gaston 2006; Villéger et al. 2008; Schleuter et al. 2010) but are used to a lesser extent in marine ecology (e.g. Paganelli et al. 2012; Wan Hussin et al. 2012; Törnroos et al. 2014). Study of community composition and diversity in terms of functional traits can provide mechanistic insight into ecosystem functioning. For example, fauna that irrigate burrows and tubes enhance sediment oxygenation, with pronounced influences on benthic respiration, nutrient flux and denitrification (Norling et al. 2007; Braeckman et al. 2010). Thus, inclusion of both taxonomic and functional trait diversity can be useful when developing comprehensive management approaches for ecosystems (Díaz and Cabido 2001; Lavorel et al. 2011).

The objective of our study was to compare and contrast the taxonomic and functional composition and diversity of macrobenthic invertebrate communities (infauna and small epifauna) in seagrass beds (eelgrass, *Zostera marina*) on the Atlantic coast of Nova Scotia, Canada. The work was conducted across a gradient of seagrass habitat that included bare sediment, the bed edge and the bed interior. Within each habitat type, we quantified the following properties of the benthic assemblages: (i) taxonomic and functional diversity, (ii) community composition based on taxonomic and functional trait structure, (iii) important species and functional traits contributing to observed patterns and (iv) the relationship between functional and taxonomic diversity. To our knowledge, this

study is one of the first to examine both the taxonomic and functional trait properties of macrobenthic invertebrate assemblages across a gradient of seagrass habitats.

Materials and Methods

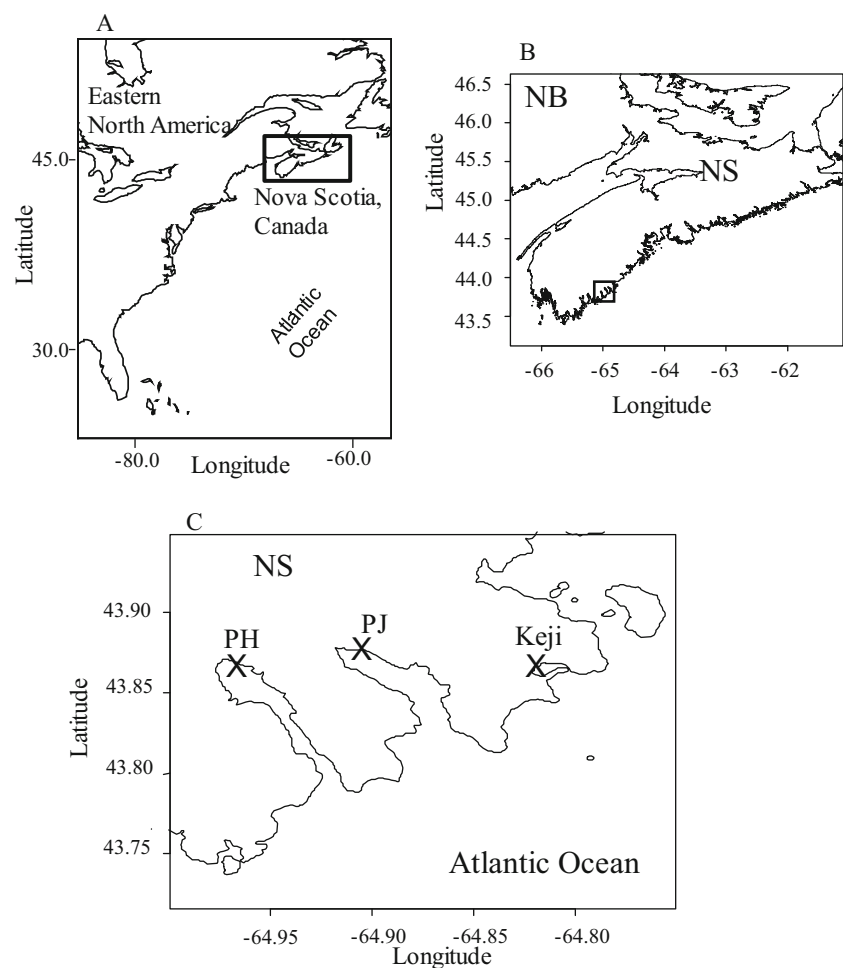
Study Sites

The study sites were located at Port l'Hebert (PH), Port Joli (PJ) and Kejimkujik National Park Seaside on the south shore of Nova Scotia (NS), Canada (Fig. 1). PH is a semi-enclosed bay with a small sill at its mouth, while PJ is a relatively more open bay that shoals from the mouth to the head of the bay. In both PH and PJ, extensive (1–2 km²) monotypic *Z. marina* (eelgrass) beds are located on elevated flats at the heads of the bays and are irrigated by a complex system of channels. The beds are typically subjected to low water currents and high sediment deposition and are continuous with little fragmentation. The water depth during mean tides ranges from 0.20 to 1.5 m, and the beds are sometimes exposed during spring low tides. The heads of the bays are surrounded by freshwater

streams that drain upland bogs, which cause moderate tannin concentrations in the water column after large rain events. Anthropogenic impacts at the study sites are limited due to minimal coastal development and the designation of the seagrass beds as migratory bird sanctuaries.

The seagrass bed at Keji is located in the innermost part of a tidal lagoon. Water flow is restricted at this location by a hydraulic constriction (caused by a bridge and causeway) between the inner and outer lagoon regions (Dowd et al. 2014). Thus, median tidal range at the seagrass bed is reduced by 30 % relative to the outer lagoon region; the water depth in the seagrass bed ranges from 0.35 to 1.0 m during mean tides (Dowd et al. 2014). Water turnover time, determined by a flushing box model based on temperature records and a heat budget, is approximately 8 days in the inner lagoon where the seagrass bed is located, while it is 1 day in the outer lagoon (Dowd et al. unpublished). The *Z. marina* bed when sampled was continuous but less extensive (0.101 km²) than the beds at PH and PJ. While the bed is dominated by *Z. marina*, some *Ruppia maritima* L. is present in the upper reaches. Extensive freshwater bogs surround the inner lagoon and cause high tannin concentration in the inner lagoon waters, particularly after large rain events. Monitoring of

Fig. 1 **a** East coast of North America. Nova Scotia is indicated by the box. **b** Region of the south shore of Nova Scotia (NS) where sampling took place (indicated by box). **c** Location of field sites in Port l'Hebert (PH), Port Joli (PJ), and Kejimkujik National Park Seaside (Keji)



seagrass cover in Keji by Parks Canada suggests a decline of ~90 % over nearly three decades (Ure et al. 2010).

Further data of physical properties (i.e. water temperature, water column chlorophyll-a and DIN and total suspended solids) and annual growth of *Z. marina* at all three sites is provided by Wong et al. (2013).

Field Sampling

Sampling took place in August 2009. At PJ and PH, three areas of the seagrass beds were sampled: bare (continuous bare area >5 m from the bed edge), edge (within seagrass, ~1 m from the edge) and interior (within seagrass and >10 m from any seagrass-bare interface). At Keji, only the bare and bed interior were sampled due to concerns regarding the impact on the already disturbed ecosystem. All sampling was conducted within a 100×100 m area and conducted at low tide by snorkelling. Ten stations within each habitat were sampled at approximately the same depth. Stations were determined haphazardly, with each station separated by at least 5 m.

At each station, a 0.25×0.25 m quadrat was used to determine shoot density by placing the quadrat on the bottom and counting all shoots within the quadrat. A 10 cm diameter wire circle was then placed over the blades within the quadrat, and all aboveground plant components were collected. A 10 cm diameter×12 cm deep hand core was then taken within the wire circle. This sampling captured both infaunal organisms within the sediment and smaller epifauna on and within the plants (e.g. amphipods). Larger mobile epifauna, such as shrimp, small fish and crabs, were not included in the sample collection. Cores to determine sediment particle size and organic content were taken using a 3 cm diameter×5 cm deep syringe core. Macrobenthic invertebrate cores and plant samples were refrigerated for ~3 days until processing, while sediment cores were frozen for ~1 month prior to analyses.

Sample Processing

In the laboratory, macrobenthic invertebrate core samples and aboveground plant components from each station were rinsed over a 0.5 mm sieve using sea water. Epifauna entangled or attached to plant components were removed and added to the sieve. Plant components were then removed for later processing. Remaining material on the sieve was fixed in 5 % buffered formalin for 2 weeks and then preserved in 70 % ethanol until sorted. Samples were sorted under a dissecting microscope, and animals were identified to the lowest possible taxonomic level (usually species, Appendix Table A1). Abundance of each species was determined for each sample.

Aboveground and belowground plant components were dried separately at 60 °C for 48 h and weighed to determine dry biomass per sample. The lengths of all third leaves in the samples were measured.

Sediment cores were analysed for organic and silt content. To determine percent organic content, 0.5 g of each sample were dried at 60 °C for 48 h, weighed to determine total dry mass, combusted at 500 °C for 7 h and reweighed to determine ash mass (Luczak et al. 1997). Percent organic content was calculated as $100 \times (\text{total dry mass} - \text{ash mass}) / \text{total dry mass}$. To determine percent silt content, 25 g of each sample was dried at 60 °C for 48 h, weighed and then mechanically stirred for 15 min with 2 g sodium hexametaphosphate to disaggregate particles (Bale and Kenny 2005). The samples were then left overnight and stirred for 15 min the following morning. The samples were then wet-sieved on a 64 µm sieve, and remaining sand on top of the sieve was dried at 60 °C for 48 h and weighed. Percent silt content was determined as $100 \times (\text{total dry mass} - \text{sand mass}) / (\text{total dry mass})$. Due to time constraints, only two replicates per habitat were processed for percent silt content of sediments.

Metrics Based on Taxonomy

Total abundance per core was determined for each seagrass habitat at each site. Taxonomic richness and diversity (hereafter referred to collectively as ‘taxonomic diversity’) per core were also determined for each seagrass habitat at each site. Taxonomic richness was measured by two indices: species richness (*SRich*) and Margalef’s index (*d*). *SRich* was determined by enumerating the total number of species present per core. *d* was calculated as

$$d = \frac{(SRich - 1)}{\log N}$$

where *N*=total number of individuals per core. This measures the number of species present relative to the number of individuals; higher values represent greater species richness.

Taxonomic diversity was calculated using the Simpson index (*Simp*):

$$Simp = 1 - \sum_i^S p_i^2$$

where *p_i* = the proportional abundance of species *i* per core, and *S* = the total number of species per core. This metric expresses how evenly individuals are distributed among the different species within the community; large values indicate all species are similar in abundance. All taxonomic indices were calculated using Primer-E v6.1.13.

Metrics Based on Biological Traits

Biological traits used in the analyses of functional trait composition and diversity were selected based on their direct or indirect influence on processes important for the ecosystem

functioning of seagrass beds. Ecosystem functions considered were nutrient cycling, sediment oxygenation, production and trophic support, habitat creation, sediment stabilization, sediment transport, benthic–pelagic coupling and carbon sequestration. Biological traits chosen were those known to influence these functions and included motility, feeding, habitat structure, sediment movement, size, form and living position in the habitat (Table 1; Snelgrove 1997; Herman et al. 1999; Pearson 2001). Specific examples of how these traits influence the ecosystem functions are provided in Appendix Table A2. Measures of fitness, migration and lifespan were not included because they are not functionally important for this study, although they could be significant in studies examining species response to disturbance (e.g. Bremner et al. 2006; Dolbeth et al. 2013). Careful selection of traits allows for functional diversity values that relate well to the study

objectives and to the prediction of ecosystem functioning (Lavorel and Garnier 2002).

Biological traits were identified for all the species listed in Appendix Table A1. Data of species traits were obtained from an available database, taxonomic texts, journal papers and personal observations during sample processing (i.e. animal sizes observed in samples) (Scheltema 1964; Sellmer 1967; Bousfield 1973; Cook and Brinkhurst 1973; Sheader 1978; Fauchald and Jumars 1979; Appy et al. 1980; Dauer et al. 1981; Ponder 1984; Oakden 1984; Fredette and Diaz 1986; Rice et al. 1986; Ulrich et al. 1995; Weiss 1995; Levin et al. 1997 and references therein; Madsen et al. 1997; Pollock 1998; Scaps 2002; Michaelis and Vennemann 2005; MarLIN 2006; Prato and Biandolino 2006). In some cases, species might only exhibit one category (e.g. medium) within a trait (e.g. body size). However, species often exhibited multiple

Table 1 Biological traits of macrobenthic invertebrates used to characterize functional diversity

Trait	Category	Description
Motility	Sedentary or moves only within a fixed tube	Species which have no or limited mobility, are attached or are limited to a tube
	Swim	Species that swim in the water column, but can return to sediment or plants
	Crawl on sediment surface or plants	Species that have limited movement on sediment surface or plants
	Motile within sediments	Infaunal species move within a burrow or freely within sediments
Feeding	Filter feeder	Removal of particulate food from water column
	Predator	Species that actively predate
	Scavenger	Feeding on dead animals
	Grazer	Scrapping or grazing live algae and plants
	Surface deposit feeder	Removal of detritus from the sediment surface
Habitat structure	Sub-surface deposit feeder	Removal of detritus from within the sediments
	Burrow	Lives within a permanent or temporary burrow
	Tube	Lives within a tube
	None, free living	Not limited to a restrictive structure, freely moves on sediment surface or within sediments
Sediment movement	Surface (top 2 cm) to deep	Translocation of sediment/particles to deeper sediments through feeding, defecation or burrowing
	Deep to surface	Translocation of sediment/particles to the surface from some depth by feeding, defecation or burrowing
	Surface mixing	Mixing at the surface (does not include deposition from filter feeders)
	No sediment mixing	No bioturbation capacity
Size	Small (0.5–5 mm)	Longest dimension
	Medium (5–20 mm)	
	Large (≥ 20 mm)	
Form	Veniform (length \gg width)	Body much longer than wide
	Globulose (length \geq width)	Body longer than wide
	Contains calcium carbonate	Contained in body or shells
Living position in habitat	On sediment surface	Location of species in sediments or on plants
	Within top 2 cm of sediment	
	Below top 2 cm of sediment	
	Attached to sediment or plant surface	
	Within plants, unattached	

categories within a trait. For example, *Nereis diversicolor* are known to be filter feeders, predators, scavengers and deposit feeders (Fauchald and Jumars 1979). To account for a taxon's ability to display multiple trait categories to varying degrees, a so-called 'fuzzy coding' procedure was used to score species traits (Chevenet et al. 1994; Bremner et al. 2006). This means that categories within a trait were assigned scores between 0 and 1, with 0 being no affinity for the trait and 1 being high affinity with the constraint that allocation of scores across a trait sum to 1. When information of biological traits was not available at the species level, data from a related species or the next taxonomic level was used if available and considered appropriate. In cases where no biological trait data were available, zero values were assigned to all traits (this occurred for three taxa in this study). The resultant trait matrix is provided in Appendix Table A3. Note that the use of binary trait coding, which removes the weighting among categories within a trait, was investigated but did not yield different results.

The biological trait information was used to calculate the Rao quadratic entropy index of functional diversity (*FD*) (Rao 1982) for each core:

$$FD = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j$$

where d_{ij} is the dissimilarity between species i and j based on trait category values calculated using Euclidian distance. If each pair of species do not share any traits (i.e. $d_{ij}=1$), then *FD* reduces to the Simpson index (*Simp* above; Lepš et al. 2006). Large *FD* values indicate that all functional traits are equally represented, and there is a high probability that two randomly chosen species are functionally different (Lepš et al. 2006). *FD* was calculated separately for each trait, and total *FD* was calculated by taking the mean of these values (Lepš et al. 2006). All species listed in Appendix Table A1 were included in the calculation of *FD*. We chose the Rao index to represent *FD* because it includes both species abundance information as well as distances among traits, both of which are important to consider when determining consequences of species loss (Petchey and Gaston 2006). We calculated dissimilarity using the 'vegan' package and *FD* using the 'Ade4' package in R v3.0.0 (R Foundation for Statistical Computing).

Functional trait composition within each habitat was explored by calculating the weighted trait category occurrence (*WTO*) for each core, as described by Bremner et al. (2006) and as represented by the following:

$$WTO = \sum_{i=1}^S p_i x_i$$

where x_i is the trait category value (i.e. 'fuzzy-coding' value) for species i . Weighting is provided by the proportional species abundance (p_i). Summation across species (S) provides a

measure of the occurrence of that trait category within each core (Bremner et al. 2006). The resultant matrix of weighted trait category occurrences by cores was utilized in ordinations (see below).

Data Analyses

For data from PJ and PH, differences in macrobenthic invertebrate abundance, diversity indices (*SRich*, *d*, *Simp*, *FD*) or habitat characteristics across habitats and sites were determined using two-way fixed factor ANOVAs. Because only two habitats were sampled at Keji (bare and interior), the data for this site were analysed separately using a one-way ANOVA to avoid an unbalanced design. Significant main effects or interactions were examined using Tukey's test. Residual plots were used to determine if the underlying assumptions of homogeneity of variance and normality were violated; any violations were corrected by weighting the analyses by the inverse of the replicate standard deviation and/or by data transformations (Draper and Smith 1998).

Relationships between *FD* and taxonomic diversity measures (*SRich*, *d*, *Simp*) were explored using regression analyses. Regressions were conducted for data pooled across habitats at each site. Based on observations of data and behaviour of the residuals, linear least squares regression (excluding the intercept) was used in most cases. For *FD* vs. *SRich* at PH and Keji and for *FD* vs. *d* at PH, analyses of the residuals indicated that non-linear relationships were appropriate. For these cases, non-linear least squares regression was used to fit the hyperbolic function:

$$FD = \frac{ax}{1 + bx}$$

where a and b are scaling and shape parameters, respectively, and x is either *SRich* or *d*. All regressions did not include an intercept parameter (i.e. regressions were forced through the origin). The purpose of these regressions was to identify general relationships between functional and taxonomic diversity and to compare these relationships across sites. R^2 values and regression statistics are provided (note that these are not entirely appropriate for non-linear regression, so only R^2 are provided for non-linear regressions and should be interpreted with caution). Regressions and ANOVAs were done using the statistical software R v3.0.0 (R Foundation for Statistical Computing).

Community composition based on taxonomy (i.e. abundance of species) and functional traits (i.e. *WTO*) were analysed separately for each site to identify differences among habitats using non-metric multidimensional scaling (nMDS). Raw data were square-root transformed and used to construct Bray-Curtis similarity matrices. These matrices were used in an nMDS analyses to construct two-dimensional ordinations.

Stress values generated from the nMDS were used to evaluate the accuracy of the ordinations, where values <0.20 indicate adequate representation (Clarke and Warwick 2001). Ordinations were followed by one-way analyses of similarities (ANOSIM) to determine if separation among habitats was evident, based on global R values and associated p values from permutation tests (where R is scaled between 0 and 1, and values approaching 1 indicated strong separation of data). If separation was evident, pairwise R values were used to determine which habitats contributed to observed separation; p values were not used at this stage because the reduced number of replicates can increase type I error, and avoidance of p values for pairwise comparisons is recommended (Clarke and Warwick 2001). Similarity percentages (SIMPER) was used to determine species or traits that contributed most to the ANOSIM results. Species or traits considered important contributors to observed differences included those that contributed $>6\%$ to the overall dissimilarity. nMDS, ANOSIM and SIMPER were conducted using Primer-E v6.1.13.

Results

General Descriptors of the Macrobenthic Invertebrate Community and Seagrass Habitat

A total of 48 taxa of macrobenthic invertebrates ($>500\ \mu\text{m}$) were observed across all sites and habitats (Appendix Table A1). Total abundance of macrobenthic invertebrates per core ranged from 18 to 320 (Fig. 2). Patterns in total abundance across habitats were site dependent (habitat \times site: $F_{2,53}=3.69$, $p=0.032$): at PH, total abundance was highest at the bed edge, while at PJ, it was highest in the bare habitat. These patterns are mainly driven by the abundance of

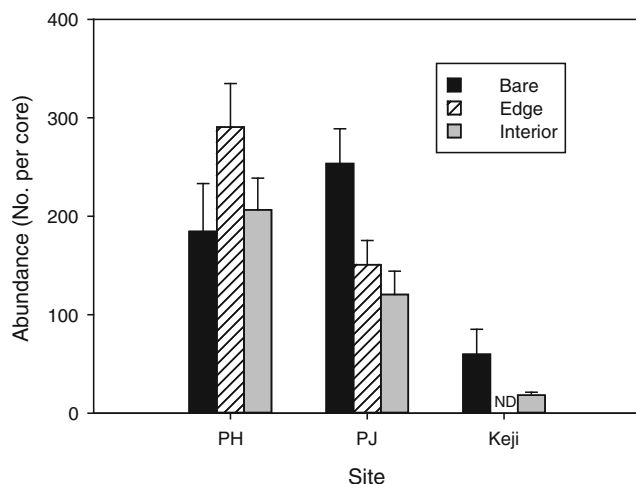


Fig. 2 Mean (+1 SE) abundance of macrobenthic invertebrates per core in seagrass habitats at each site. See Fig. 1 for site abbreviations. ND no data, $n=10$

gastropods and bivalves (Appendix Table A1). The separate analyses conducted at Keji indicated that total abundance did not differ significantly across bare habitat and the bed interior (habitat: $F_{1,18}=2.63$, $p=0.122$), although there is a suggestion of higher abundance in bare habitat relative to bed interior (Fig. 2). Polychaetes and amphipods were the main contributors to overall abundance at Keji (Appendix Table A1).

At PJ and PH, seagrass shoot density and aboveground and belowground biomass were consistently higher in the interior of the seagrass beds compared to the bed edge (habitat: $F_{1,36}=6.28$ – 19.0 , $p=0.017$ – 0.0001 ; Fig. 3a–c). Similarly, the length of the third leaf was consistently longer in the bed interior than the bed edge (habitat: $F_{1,225}=29.6$, $p<0.0001$; Fig. 3d). Shoot density at Keji was much lower than at PH and PJ (64 shoots m^{-2}), while leaf length was much higher (830 mm). The longer leaf length at Keji lead to aboveground biomass similar to that observed at PH and PJ, despite the low shoot density. Belowground biomass at Keji in the bed interior was less than that in the bed interior of PH and PJ.

Percent silt content of sediments differed significantly between PH and PJ and ranged from 40 to 50 % at PH and 50 to 65 % at PJ (site: $F_{1,6}=6.74$, $p=0.041$; Fig. 3e). Silt content of sediments did not change significantly across seagrass habitats at any site. At PH and PJ, percent organic content of sediments ranged from 15 to 40 % and was highest in the bed edge at both sites (habitat \times site: $F_{2,54}=3.43$, $p=0.039$; Fig. 3f). Percent organic content was similar at Keji in both bare habitat and the bed interior ($F_{1,18}=0.658$, $p=0.428$).

Taxonomic and Functional Diversity

At both PH and PJ, taxonomic richness ($SRich$ and d) differed significantly across seagrass habitats (habitat: $F_{2,53}=18.1$, $p<0.0001$ and $F_{2,53}=27.5$, $p<0.0001$ for $SRich$ and d , respectively; Fig. 4a, b). For $SRich$ at PH and PJ, post hoc comparisons indicated that the bare habitat was significantly lower in taxonomic richness than the bed edge and interior, which did not differ from each other. Examination of the data also suggests that $SRich$ in the bed edge was lower than in the bed interior, although this result was non-significant in post hoc comparisons. d was significantly lowest in the bare habitat, intermediate in the bed edge and significantly highest in the bed interior at both PH and PJ. At Keji, $SRich$ and d did not change significantly across habitats, although d tended to be higher in the bed interior.

The relationship between Simpson diversity index ($Simp$) and seagrass habitats was dependent on site (habitat \times site: $F_{2,53}=7.18$, $p=0.002$; Fig. 4c). At PH, $Simp$ was significantly lowest in bare habitat compared to the bed edge and interior. At PJ, $Simp$ was significantly lowest in bare habitat, intermediate in bed edge and significantly highest in the bed interior. At Keji, $Simp$ was significantly higher in the bed interior compared to the bare habitat ($F_{1,18}=4.85$, $p=0.041$).

Fig. 3 Mean (± 1 SE) plant and sediment properties in seagrass habitats at each site. See Fig. 1 for site abbreviations. *ND* no data, $n=10$ (a–e), $n=2$ (f)

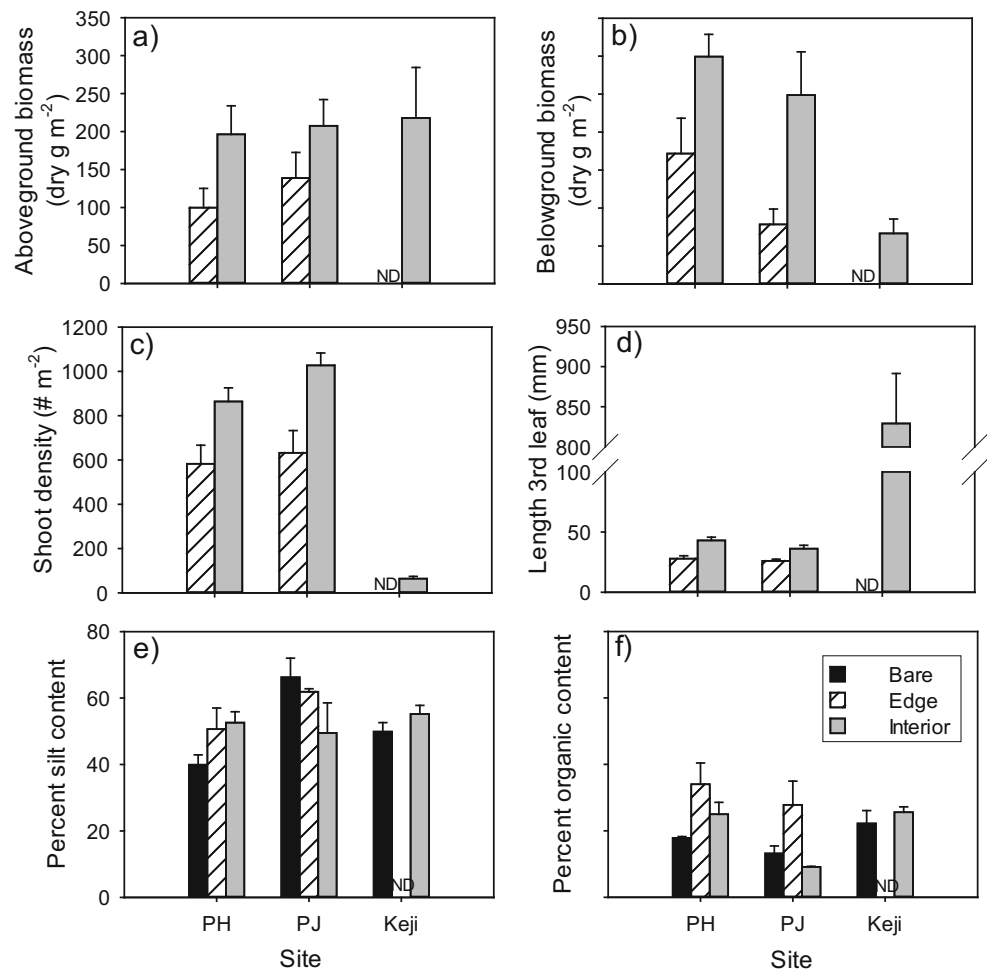
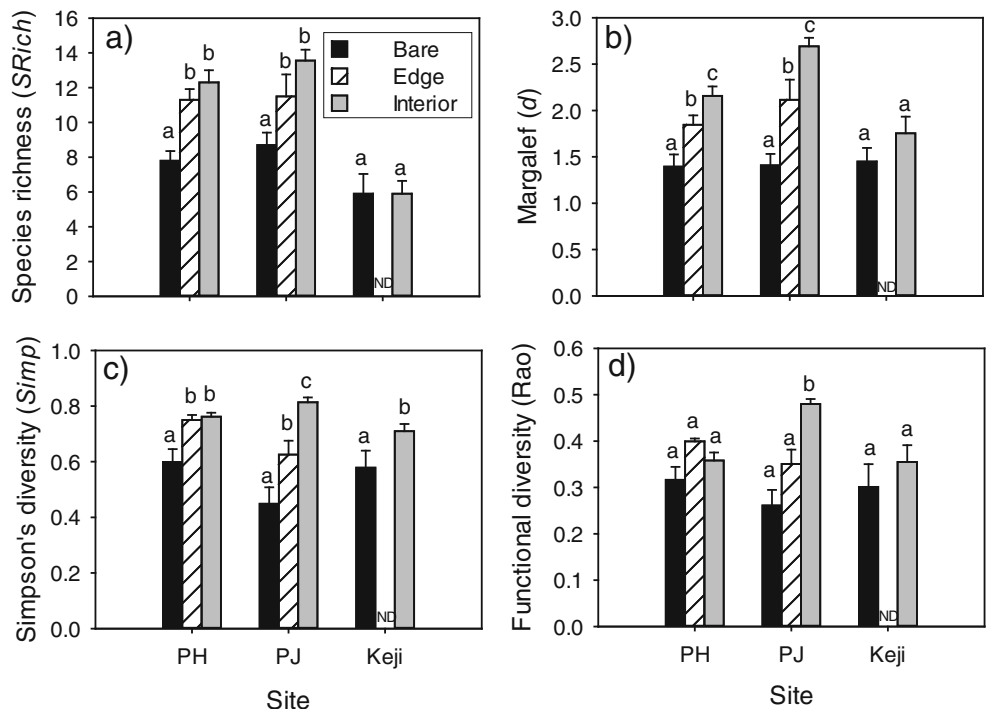


Fig. 4 Mean (± 1 SE) taxonomic and functional diversity indices of macrobenthic invertebrates per core in seagrass habitats at each site. Indices include **a** species richness (*SRich*), **b** Margalef index *d*, **c** Simpson's index (*Simp*), and **d** total functional diversity (*FD*) measured by Rao's quadratic entropy index. Total *FD* was determined as the mean of *FD* for the individual traits shown in Fig. 5. Results of post hoc comparisons within each site are indicated by the letters above each bar, with different letters indicating significant differences between habitats. See Fig. 1 for site abbreviations. *ND* no data, $n=10$



The relationship between total *FD* and seagrass habitat was dependent on site (habitat \times site: $F_{2,53}=15.85$, $p<0.0001$; Fig. 4d). At PH, *FD* did not differ significantly across seagrass habitats as it did for taxonomic diversity. At PJ, *FD* was significantly lowest in bare habitat and bed edge compared to the bed interior. This pattern is similar yet less strong than that for taxonomic diversity, which typically differed across all three habitats. At Keji, *FD* did not differ between bare habitat and the bed interior ($F_{1,18}=0.801$, $p=0.383$). Similar to patterns for *Simp* and *SRich* at Keji, *FD* tended to be higher in the bed interior relative to the bare habitat; yet, this result was not statistically significant.

At PH and PJ, *FD* calculated for each trait showed similar patterns across habitats to total *FD* for the traits sediment movement and size (both PH and PJ), living position (PJ only), and feeding and habitat structure (PH only) (habitat \times site: $F_{2,53}=2.97$ – 11.05 , p 0.060– <0.0001 ; Fig. 5). At Keji, *FD* of all traits were similar across bare habitat and the bed interior ($F_{1,18}=0.02$ to 1.86 , $p=0.89$ to 0.189), with the exception of feeding, which had higher *FD* in seagrass than in the bare ($F_{1,18}=5.19$, $p=0.035$). Almost all trait categories were present within all habitats and sites (Appendix Figure A1–A3).

Positive increasing relationships between *FD* and all indices of taxonomic diversity were evident (Fig. 6a–f). Regression between *FD* and *SRich* was linear at PJ ($p<0.0001$, $R^2=0.937$). At PH and Keji, a saturation effect in *FD* at high *SRich* was evident ($R^2=0.190$ and 0.255 , respectively). A hyperbolic curve was also fit for *FD* vs. d at PH ($R^2=0.206$), while the relationship was linear at both Keji ($p<0.0001$, $R^2=0.864$) and PJ ($p<0.0001$, $R^2=0.956$). Linear relationships between *FD* and *Simp* were evident at all sites (PH: $p<0.0001$, $R^2=0.989$; PJ: $p<0.0001$, $R^2=0.998$; Keji: $p<0.0001$, $R^2=0.877$). The estimated slope parameters suggest that the slopes did not differ greatly among sites for *FD* vs. *Simp*, although a fair amount of variation in the data was evident at Keji.

Community Structure Based on Species Taxonomy and Functional Traits

The nMDS ordinations of community structure based on taxonomic abundance showed clear separation of habitats at both PH and PJ (global $R=0.507$, $p=0.001$ and 0.695 , $p=0.001$ for PH and PJ, respectively; Fig. 7a, b). At PH, pairwise habitat comparisons of bare to interior and edge to interior were strongly different (pairwise $R=0.790$ and 0.500 , respectively). SIMPER results indicated that species contributing to these differences included gastropods (*Littorina* sp., *Hydrobia minuta*, *Onoba aculeus*), a bivalve (*Gemma gemma*), Oligochaetes and the polychaete *Capitella capitata*. Bare and edge were also separated at PH (pairwise $R=0.310$), although less strongly so, given the variation observed for data in bare habitat.

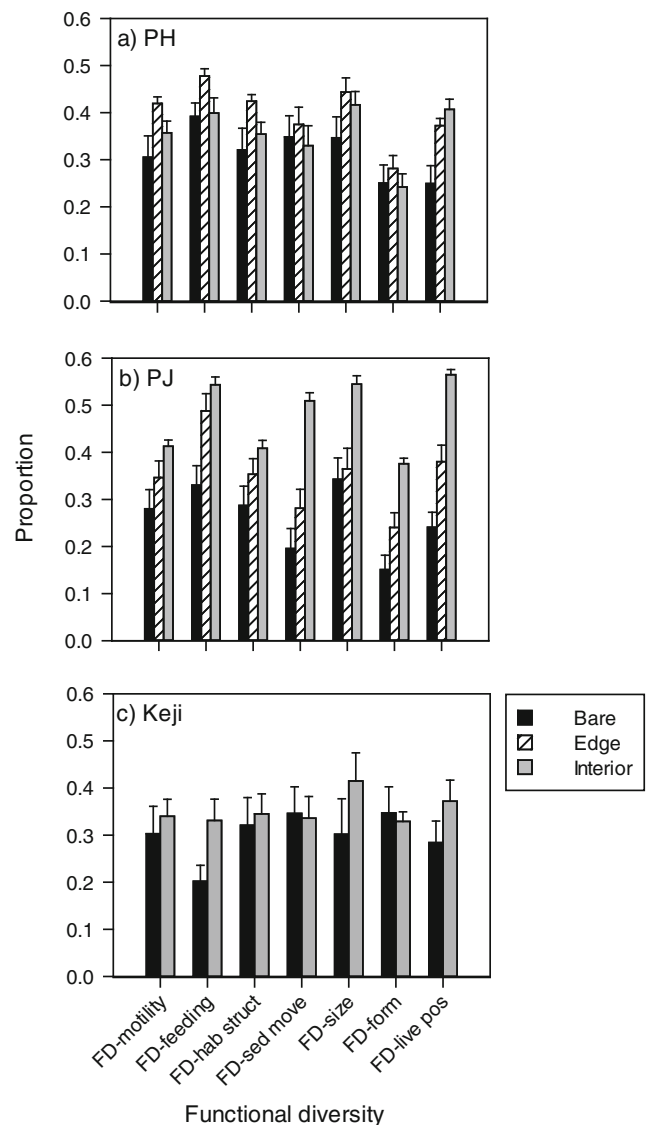
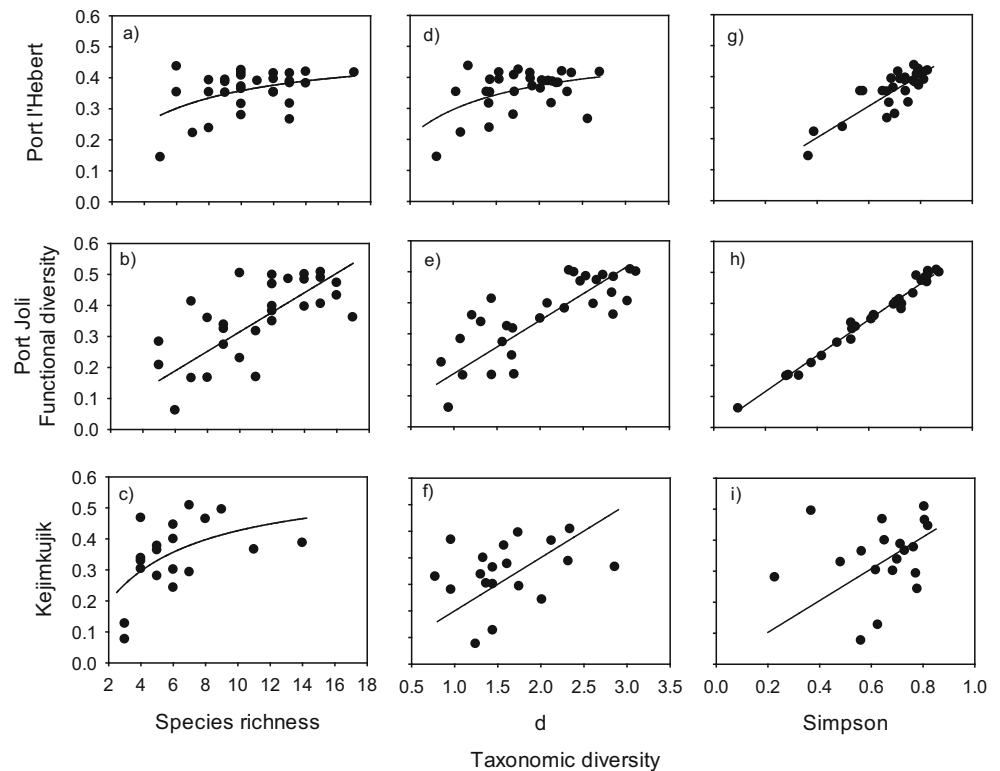


Fig. 5 Mean (± 1 SE) functional trait diversity (*FD*) of macrobenthic invertebrates per core in seagrass habitats at each site. *hab struct* habitat structure, *sed move* sediment movement, *live pos* living position. See Fig. 1 for site abbreviations. $n=10$

At PJ, all habitat comparisons differed in community structure when based on taxonomic abundance (pairwise $R=0.424$, 0.973 , 0.814 , for bare to edge, bare to interior and edge to interior comparisons, respectively). Species contributing to differences between bare and edge, and bare and interior, were the same as those observed at PH. Species contributing to the difference in community structure between the edge and interior included the bivalve *G. gemma*, gastropods (*Littorina obtusata*, *Acteocina canaliculata*), Oligochaetes and a spionid polychaete (*Streblospio benedicti*).

The nMDS ordination of community structure at Keji indicated that habitats were separated (global $R=0.362$, $p=0.001$) when based on species taxonomy (Fig. 7c). Species contributing to the separation between bare and interior habitats included polychaete worms (*C. capitata*, *Polydora ligni*),

Fig. 6 Regressions of functional diversity and various indices of taxonomic diversity for macrobenthic invertebrates pooled across seagrass habitats at each site. $n=20\text{--}30$. See text for fit statistics. Estimated parameters: **a** $a=0.12\pm0.05$, $b=0.25\pm0.14$, **b** slope= 0.032 ± 0.002 **c** $a=0.14\pm0.06$, $b=0.24\pm0.16$, **d** $a=0.71\pm0.28$, $b=1.39\pm0.78$, **e** slope= 0.172 ± 0.007 , **f** slope= 0.20 ± 0.018 , **g** slope= 0.51 ± 0.009 , **h** slope= 0.58 ± 0.004 , **i** slope= 0.51 ± 0.04



Oligochates, amphipods (*Gammarus mucronatus*, *Corophium insidiosum*) and the bivalve (*G. gemma*).

Ordinations of functional trait composition at PH and PJ showed similar separation across seagrass habitats as for taxonomic composition, although separations were sometimes less well defined (Fig. 7d, e). At PH, functional trait composition differed across habitats (Global $R=0.351$, $p=0.001$) with the interior being separated from bare and edge habitat (pairwise $R=0.579$ and 0.384 , respectively). Contrary to ordinations based on taxonomic composition, bare and edge habitats were not well separated (pairwise $R=0.122$). Important trait categories leading to differences between the bare and interior included grazing, movement within sediments, living in burrows, filter feeding, living in top 2 cm of sediment, living in plants and crawling on sediment or plants. Trait categories leading to differences between edge and interior included filter feeding, moving within sediments, living in burrows and living in top 2 cm of sediment. Weighted trait occurrence at each site is presented in Appendix Figure A1–A3.

At PJ, functional trait composition also differed across habitats (Global $R=0.662$, $p=0.001$), with the interior being separated from the bare and edge habitats (pairwise $R=0.973$ and 0.942 , respectively). Similar to PH, bare and edge habitats were not separated (pairwise $R=0.095$). Important trait categories in the bare habitat and bed interior leading to differences included filter feeding, movement within sediments, living in burrows and surface sediment mixing.

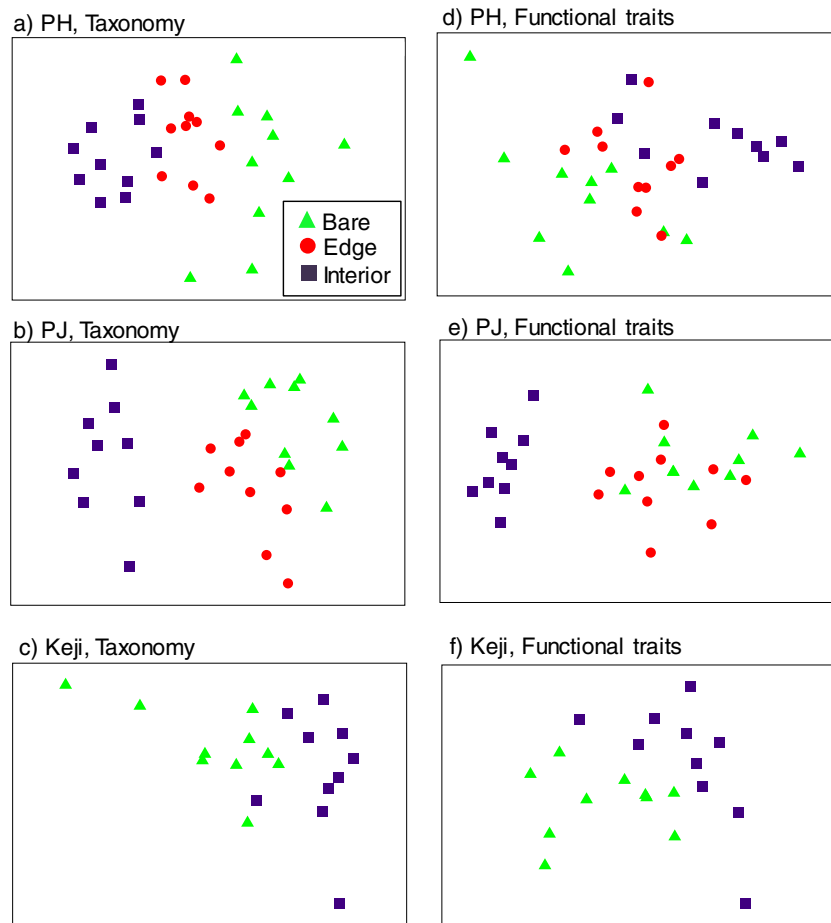
At Keji, separation of habitats based on functional trait composition was similar to when ordinations were based on

taxonomic abundance, with bare and interior habitat separated (Global $R=0.344$, $p=0.002$; Fig. 7f). Traits contributing to this difference included large size, being sedentary and living in tubes.

Discussion

Our study showed that patterns of taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats differed depending on the site. At PH and PJ, taxonomic diversity increased from the bare sediments to the bed interior. However, FD did not differ among seagrass habitats (i.e. PH) or showed a weaker pattern across habitats relative to taxonomic diversity (i.e. PJ). These results suggest that while taxonomic diversity of macrobenthic invertebrates may depend on the presence and abundance of *Z. marina* plants, functional trait diversity may show a lesser dependence or none at all. Interestingly, the difference in patterns of taxonomic and functional diversity across seagrass habitats was only observed at PH and PJ, sites relatively undisturbed and characterized by high seagrass density. At Keji, where a hydraulic constriction drastically reduced flushing rate and likely caused very low seagrass density (Wong et al. 2013), patterns in taxonomic and functional diversity across seagrass habitats were similar. Low species richness and the absence or low abundance of species and traits associated with the macrophyte environment likely contributed to this result. A variety of relationships of taxonomic and functional diversity with habitat gradients

Fig. 7 nMDS ordination plots of macrobenthic invertebrate composition across seagrass habitats based on species taxonomy (a–c) and functional traits (d–f). Stress values were all <0.2. See Fig. 1 for site abbreviations



have been observed in other marine studies. For example, Paganelli et al. (2012) found a positive relationship between *FD* (measured by Rao) and distance from the river mouth, while the opposite was observed for taxonomic diversity (measured by Shannon-Weiner). Wan Hussin et al. (2012) found that both taxonomic richness (measured by *SRich* and *d*) and *FD* (measured by Rao) were lowest at high impact dredging sites relative to reference sites. Similar to our results for Keji, Dolbeth et al. (2013) found that reduced seagrass density (caused by eutrophication) resulted in no difference in taxonomic or functional diversity between seagrass and a nearby mudflat, contrary to differences in both diversity measures between habitats when seagrass density was higher. The combination of results from the literature and our study suggests that taxonomic diversity cannot always be assumed a direct surrogate of functional diversity. This has important implications for conservation and management programs that often maintain biodiversity under the implicit assumption that ecological function will also be maintained. Such programs would benefit by establishing relationships between taxonomic diversity and *FD* in order to better predict the implications of species loss or elevation for ecosystem functioning. Although this relationship is critically

important and relevant for management programs, it remains poorly understood for most coastal ecosystems (Micheli and Halpern 2005).

In our study, we found that the relationship between taxonomic diversity and *FD* of macrobenthic invertebrates was not only influenced by site but also by the metric used to represent taxonomic diversity. Non-linear relationships best described the relationship between *SRich* and *FD* at PH and Keji and also for *d* and *FD* at PH, indicating that *FD* sometimes plateaus as taxonomic richness increases. In contrast, linear relationships were found between *FD* and Simpson's at all sites. However, the strong linear relationships exhibited are perhaps not surprising, given that the Rao index is closely related to Simpson's index (Lepš et al. 2006). Regardless, all of our relationships suggest that loss of taxonomic diversity will result in loss of *FD*. The rate of loss results from different levels of functional trait redundancy, the number of traits included within the *FD* index and the relationship between functional uniqueness and species abundance (Díaz and Cabido 2001; Petchey and Gaston 2006; Petchey et al. 2007). This last aspect is particularly interesting in that *FD* could increase with species loss if functionally unique species are higher in abundance relative to less unique species (Petchey and Gaston 2006). Thus, a positive increasing relationship between *FD*

and taxonomic diversity, although prevalent in our study, and often assumed universal, might not always hold.

Examination of species and functional trait composition provides information on the range and distribution of species and functional traits and how they relate to environmental variables. We found that patterns in species composition across seagrass habitats (bare sediment and bed edge and interior) were generally consistent with patterns in functional trait composition, although some habitat separations were weaker when ordinations were based on functional traits. Several other studies have shown a variety of relationships between taxonomic and functional trait composition (Bremner et al. 2006; Wan Hussin et al. 2012; Dolbeth et al. 2013). In our study, functional trait composition differed across seagrass habitats at all sites, particularly between the bare habitat and bed interior. Thus, although overall trait diversity may not differ between habitats (as observed at PH), different suites of functional traits may be expressed across the seagrass landscape. This suggests that, depending on the relative abundance of trait expression, some ecosystem functions derived from macrobenthic invertebrates may differ across habitats.

Potential linkages between expressed functional traits and subsequent ecosystem functions can be inferred from knowledge of the weighted functional trait values within each habitat (i.e. *WTO*; Appendix Figure A1–A3). In our study, filter feeding was more prevalent in bare habitat than the bed interior at PH and PJ, suggesting the relative importance of benthic-pelagic coupling by benthic fauna when seagrass is absent or low in density. Not surprisingly, grazing was most prevalent in the bed interior at all three sites, implying enhanced primary production. Movement in sediments and living in burrows were most prevalent in the bare habitat relative to the bed interior at PH and PJ, suggesting enhanced sediment oxygenation and nutrient cycling from the activities of macrobenthic invertebrates. At Keji, more large animals and tubes in the bed interior relative to the bare sediment may have also enhanced sediment oxygenation and nutrient cycling. Experimental manipulations of *FD* combined with measurement of processes such as respiration, nutrient flux and denitrification (e.g. Norling et al. 2007; Braeckman et al. 2010) can provide more direct linkage of functional traits with ecosystem functions, although these would be difficult in large-scale studies. Regardless, even in the absence of direct quantitative measurements, knowledge of *FD* and functional trait composition can still provide valuable insight into ecosystem functioning. In particular, *FD* studies are likely useful when relative differences are of interest, such as changes in *FD* across gradients of habitat or anthropogenic stressors or over the large timescales associated with long-term monitoring.

In conclusion, our study showed that patterns in functional diversity across seagrass landscapes may not always reflect patterns in taxonomic diversity. We also showed that regardless of the presence or absence of habitat-specific patterns in

diversity, functional trait composition tended to be distinct across different seagrass habitats. Relationships identified between various indices of taxonomic diversity and *FD* are particularly valuable to predict consequences of species loss for *FD*, and by extension, ecosystem functioning. Because our results are likely most applicable to seagrass ecosystems of the type sampled (i.e. shallow, muddy, highly depositional beds, disturbed and undisturbed), further exploration of taxonomic and functional diversity across a larger gradient of seagrass ecosystems would be beneficial. This study is valuable in that it provides some of the first information of the various relationships between taxonomic and functional diversity that may occur across gradients of seagrass habitat. This was achieved using some of the first macrobenthic invertebrate diversity information available for seagrass ecosystems in Atlantic Canada. Further diversity studies within coastal ecosystems that incorporate aspects of both species identity and functional characteristics will prove useful to inform management objectives and practices.

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