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ARTICLE

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Effects of *Spartina alterniflora* invasion on the benthic invertebrate community in intertidal wetlands

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Abstract

Exotic species invasions have profound effects on native ecosystems, with the ecological effects of non-native plants being especially pervasive. We investigated the impacts of a plant invasion on benthic invertebrate assemblages in intertidal wetlands of the Yellow River Delta, comparing benthic communities associated with exotic *Spartina alterniflora* against those associated with native plants (*Tamarix chinensis*, *Suaeda salsa*, and mudflat). Our study surprisingly found that the density, diversity, and richness of benthic invertebrates associated with *S. alterniflora* were higher than with native habitats. Multivariate analysis also revealed that the structure of benthic invertebrates in *S. alterniflora* habitats was different than in *T. chinensis* and mudflat habitats. The structure of invertebrates associated with the invasive *S. alterniflora* and native *S. salsa* was more similar, although the dominant species differed. Indicator species analyses indicated that each habitat was characterized by unique taxa. *S. alterniflora* invasion increased the beta diversity of the community, with the species turnover component being of most importance. Mollusks were most likely to be influenced by *Spartina* invasions. Given the extent of the *S. alterniflora* invasion in the Yellow River Delta, altered benthic invertebrate communities will likely have important implications for the ecology of the intertidal wetland ecosystems and deserve increased attention.

KEYWORDS
biological invasion, community structure, mollusk, the Yellow River Delta, turnover

INTRODUCTION

Intertidal wetlands are diverse, complex habitats that provide an ecologically important buffer between rivers and oceans, and often harbor unique biodiversity (Alp & Le Pichon, 2020; Kirwan & Megonigal, 2013; Noh et al., 2019). Intertidal wetlands are characterized by connectivity dynamics that are influenced primarily by tidal influences, with daily tidal dynamics driving environmental variability and creating high spatiotemporal habitat heterogeneity (Alp & Le Pichon, 2020; Tonolla et al., 2010). The dynamic nature of intertidal zones can increase their susceptibility to biological invasion and bioturbation, particularly by non-native plants. Invasive species are widely recognized as one of the primary threats to biodiversity in various habitats, including wetlands (Blanco et al., 2021; Carbonell et al., 2017; Collinge et al., 2011; Flood et al., 2020). Invasive species can influence biodiversity, resulting in ecosystem imbalances and

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detrimentally impacting natural-wetland landscape succession (Grosholz, 2002; Wigginton et al., 2014). Currently, there is an increasing concern about the colonization and ecological effects of non-native species, such as *Spartina alterniflora*, on intertidal ecosystems.

Spartina alterniflora has a dense rhizome system that binds coastal mud and its sturdy stem decreases wave action allowing silt deposition, causing elevation of the mudbank. As a result, it was widely planted at coastal sites, where it has naturally colonized large areas of tidal mudflats, becoming an invasive species. By providing new resources and mediating ecological interactions for organisms, the invasion of *S. alterniflora* likely alters habitat complexity (Pagliosa & Lana, 2005). These invasions can significantly alter the early stages of invasion, influencing flora and fauna communities' abundance, richness, and composition (Loke & Todd, 2016; Reis et al., 2019; Wolters et al., 2018). Habitat complexity may provide more resources and refugia for species, favoring stochasticity in colonization (Petsch et al., 2017), and ultimately positively or negatively impacting species populations by modifying community structure (Bezemer et al., 2014). For instance, roots provide physical support for tube builders like polychaetes, while dead aboveground material serves as food for detritivorous organisms, such as crabs (Pennings & Bertness, 2001). Natural habitats and their complexity would be altered by *S. alterniflora* invasion, resulting in displacement of other biology, including benthic invertebrates.

Benthic invertebrates play a pivotal role in many ecosystem services within coastal intertidal habitats (Bongiorni et al., 2018; Pingram et al., 2014; Wu et al., 2021). For example, benthic invertebrates are important food resources for waterbirds and fishes in intertidal wetlands (Chen et al., 2016). Numerous studies have focused on the effects of altering hydrological connectivity on benthic invertebrate assemblages (Dou et al., 2020; Wu et al., 2020; Yang et al., 2019), and benthic invertebrates can be used as indicators of intertidal wetland conditions (Griffiths et al., 2007; Weilhoefer, 2011). Recently, the effects of *S. alterniflora* invasion on benthic invertebrate communities have attracted considerable attention (Quan et al., 2016). For example, Yan et al. (2020) identified positive ecosystem engineering effects of *S. alterniflora* invasion on invertebrate biodiversity. In comparison, another reported that salt marshes dominated by *S. alterniflora* had reduced the biodiversity of benthic invertebrates (Kang et al., 2007). Thus, the effects of *S. alterniflora* invasion on benthic invertebrates may be taxon-specific, relating to the different habitats of the organisms (Wang et al., 2015).

Understanding the diversity of benthic invertebrates of the intertidal wetland habitats after the *S. alterniflora* invasion is important to understanding how intertidal ecosystems function and how its processes are important for managing estuarine wetland ecosystems. Beta diversity has long been used to analyze community composition and structural patterns along gradients (e.g., environmental, spatial, and temporal) and is essential for understanding the mechanisms that influence species' distributions (Castro et al., 2019; Jankowski et al., 2009). Beta diversity can be partitioned into the two components of nestedness and turnover, revealing the distinct contributions of these two fundamental mechanisms (Baselga, 2010). Turnover indicates that species tend to replace each other along spatial or environmental gradients, while the nestedness component represents a differential richness pattern (Baselga, 2012; Legendre, 2014). Generally, species turnover may reflect species sorting by environment or dispersal processes, whereas nestedness is often related to ordered extinction–colonization dynamics (Soininen et al., 2018).

The goal of vegetation planting in the Yellow River Delta (YRD) is to maintain the natural spatial succession, forming clear vegetation belts roughly in the pattern "mudflat–*Suaeda salsa*–*Tamarix chinensis*" progressing inland away from the ocean (Zhang et al., 2016). Since *S. alterniflora* was artificially introduced to the YRD in 1990, *S. alterniflora* has become widely distributed across its intertidal zone (Yang et al., 2017). The patterns of zonation by invasive *S. alterniflora* have reshaped local landscapes. These intertidal gradients can control patterns of benthic invertebrate community zonation (McLachlan et al., 2019). In this study, we targeted an area of the YRD where an ongoing *S. alterniflora* invasion was occurring. We predicted that despite active tidal flows among habitats and the consequent free dispersal of organisms, *S. alterniflora* invasion would still result in significant spatial variation in the distribution and diversity of invertebrate communities. The main objective of this study was to characterize the benthic invertebrate assemblages along a gradient of vegetative habitat in intertidal wetlands of the YRD after *S. alterniflora* invasion.

MATERIALS AND METHODS

Study area

This study was carried out in the intertidal wetlands of the YRD located in Dongying City, Shandong Province, China. We chose a natural tidal creek in the YRD, with clear vegetation belts roughly in the pattern "*S. alterniflora*–mudflat–*S. salsa*–*T. chinensis*" progressing inland away from the ocean (Figure 1). These natural intertidal vegetation gradients maintain high hydrological connectivity. Due to the daily tidal dynamics, *S. alterniflora* tends to keep continually invade in the direction of land. This region has a warm-temperate continental monsoon climate with four distinct seasons and a rainy summer. The average annual precipitation is 530–630 mm, of which about 70% is concentrated in summer (Fan et al., 2012), and the annual mean

temperature ranges from 11.5 to 12.4°C (Kong et al., 2015). The main soil types in the study area were fluvo-aquic and saline soils. The dominant native species were the herbaceous plants *S. salsa* and *T. chinensis* (Gao et al., 2015).

Field and laboratory methods

Considering the tidal influence, sampling accessibility, and *S. alterniflora* growth stages, benthic invertebrate communities were sampled along the vegetation gradients in intertidal wetland habitats of the YRD in April and July 2019: (1) *T. chinensis* habitats ($n = 4$), (2) *S. salsa* habitats ($n = 4$), (3) mudflat habitats ($n = 4$), and (4) *S. alterniflora* habitats ($n = 4$). Invertebrates that occur on plants and the soil surface were sampled at each study site using a 1-mm mesh D-shaped net with a 35-cm-diameter opening. The net was dragged 1 m horizontally from the interior of the water body to the shore, scraping the bottom of the net along the benthic surface (Batzer et al., 2001). Meanwhile, in each habitat, invertebrates that occurred in the soils (up to 5 cm depth) were sampled using a shovel in quadrat plots of 20 × 25 cm (0.05 m^2) and then sieved in situ with 0.5-mm mesh sieves. These complimentary sampling methods better ensured that the full range of organisms present was sampled. Specifically, four 1-m-long horizontal sweeps and four 20 × 25-cm

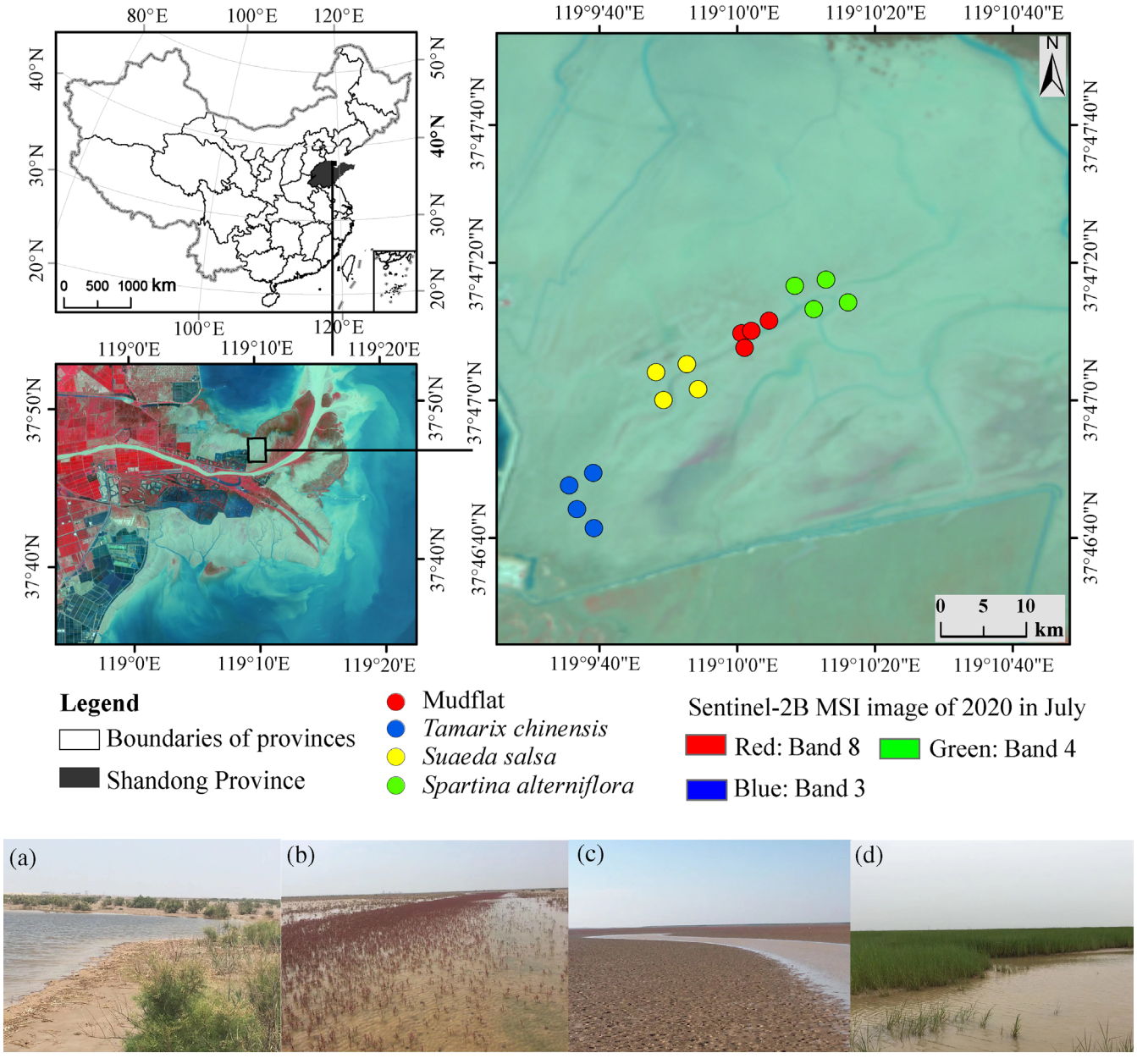


FIGURE 1 Sampling sites among each habitat in intertidal wetlands of the Yellow River Delta. (a) *Tamarix chinensis* habitats; (b) *Suaeda salsa* habitats; (c) mudflat habitats; (d) *Spartina alterniflora* habitats

TABLE 1 Average abundance (individuals/m^2) of benthic invertebrate family among each habitat in the intertidal wetlands of the Yellow River Delta in April and July 2019

			Tamarix chinensis		*Suaeda salsa*		Mudflat		*Spartina alterniflora*	
Phylum	**Class**	**Family**	**April**	**July**	**April**	**July**	**April**	**July**	**April**	**July**
Arthropoda	Malacostraca	Amphithoidae	0.89 (1.35)	0.54 (0.68)	0.89 (1.35)	0	0	0	0	0.18 (0.36)
		Corophiidae	0	0	1.78 (2.64)	0	0	0	45.00 (44.88)	6.07 (12.14)
		Corallanidae	0	0	0	0	0	0	0	0.18 (0.36)
		Hyalidae	0	0	0.18 (0.36)	0	0	0	2.50 (3.71)	0
		Leucosiidae	0	0	0	0	0	0	0.18 (0.36)	0.18 (0.36)
		Mysidae	0	0	0	0	0	0	2.68 (4.46)	0
		Macrophthalmidae	0	0	2.50 (5.00)	11.25 (11.09)	3.75 (4.79)	8.75 (4.79)	0	13.75 (6.29)
		Oniscidae	0.18 (0.36)	0.18 (0.36)	0	0	0	0	0	0
		Palaemonidae	0.71 (1.01)	1.79 (3.11)	0	25.89 (31.79)	0	0	0.36 (0.71)	6.07 (5.79)
		Sergestidae	24.82 (20.34)	50.89 (37.25)	5.18 (3.97)	5.89 (11.79)	0	0	4.11 (3.84)	16.96 (25.96)
		Varunidae	2.50 (2.89)	0.36 (0.41)	15.0 (10.80)	0	7.50 (6.45)	3.75 (4.79)	5.00 (7.07)	5.18 (6.91)
Annelida	Polychaeta	Goniadidae	0	0	5.00 (7.07)	0	11.25 (16.52)	8.75 (7.50)	7.50 (11.90)	0.36 (0.71)
		Nereididae	0	0	1.60 (2.36)	0	5.00 (4.08)	2.50 (2.89)	0	5.00 (7.07)
		Scolecida	0	0	0	0	0	5.00 (4.08)	1.25 (2.50)	1.25 (2.50)
Mollusca	Bivalvia	Alvenius	0	0	61.25 (43.47)	18.75 (22.50)	0	0	41.25 (43.28)	271.25 (193.06)
		Pharidae	0	0	0	0	0	0	2.68 (1.97)	1.07 (2.14)
		Semelidae	0	0	0	1.79 (2.22)	0	0	1.42 (2.86)	2.86 (3.50)
		Veneridae	0	0	0	0	0	0	0	0.36 (0.71)
		Veneroida	0	0	1.43 (2.86)	1.25 (2.50)	0	0	1.43 (1.30)	0
	Gastropoda	Assimineidae	0	0	0.54 (0.68)	0	0	0	1.61 (1.88)	0.54 (0.68)
		Bithyniidae	0	0	0	0	0	0	15.54 (31.07)	24.46 (48.93)
		Cochlicopidae	0	0	0.71 (0)	5.18 (3.42)	0	0	0	0
		Hydrobiidae	0.36 (0.71)	0.18 (0.36)	9.82 (5.45)	136.25 (76.57)	0	0	20.54 (31.87)	9.29 (11.17)

(Continues)

TABLE 1 (Continued)

Phylum	Class	Family	*Tamarix chinensis*		*Suaeda salsa*		Mudflat		*Spartina alterniflora*	
			April	July	April	July	April	July	April	July
		Hydrobiidae	0	0	0.18 (0.36)	0	0	0	0	0
		Lymnaeidae	0	0	0	0	0	0	0	2.86 (5.71)
		Naticidae	0	0	0	1.43 (1.54)	0	0	0	0
		Pyramidellidae	0	0	9.64 (3.93)	0	0	0	0	0
		Stenothyridae	0	0	5.36 (3.76)	2.32 (3.05)	0	0	18.04 (16.04)	12.86 (15.15)
		Viviparidae	0	0	0	0	0	0	0	1.61 (3.21)

Note: Data are shown as mean ± SD.

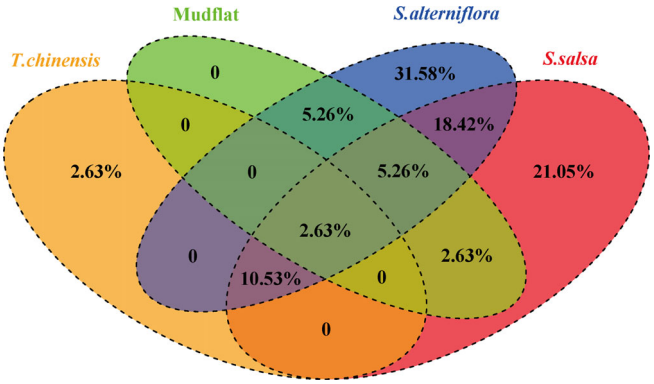


FIGURE 2 Venn diagram of taxonomic overlap (%) of benthic invertebrate assemblages among each habitat in intertidal wetlands of the Yellow River Delta (38 taxa in total)

quadrat plots were collected at randomly selected locations at each sampling site. All four net sweeps using a shovel quadrat per sampling site were pooled and added to a labeled plastic bag, respectively. Overall, we collected two samples (one net and one soil) per plot (four) per date (two) in each habitat (four), totaling 64 samples for four habitats, consisting of 32 sweep samples and 32 soil samples. All the samples were preserved in 95% ethanol and transported back to the laboratory. Using a portable meter (YSI-556MPS, USA), the water salinity was measured in each intertidal wetland habitat.

In the laboratory, organisms from each sample were sorted, identified using a stereomicroscope, and counted. Organisms were identified to the lowest taxonomic level possible, and the numbers of benthic invertebrates in the sample area were enumerated.

Data analysis

The Kruskal–Wallis *H* test was used to assess the differences between habitats in species density, and the diversity indexes of benthic invertebrates. Base data were calculated by using Excel 2010. Figures were plotted using Origin version 2018 and ArcGIS software (version 10.1, USA).

To visualize the variabilities in benthic invertebrate assemblages and to identify possible groupings among the different sites, nonmetric multidimensional scaling (NMDS) ordinations were used to investigate differences in benthic invertebrate community composition among groups. The analysis of similarities (ANOSIM) was conducted based on the Bray–Curtis dissimilarity matrix to test the significance of differences among different groups. Similarity percentage (SIMPER) analyses were used to determine the particular taxa responsible for differences among groups. These analyses were run in PRIMER 7.0 (Clarke & Gorley, 2015).

To identify the representative species within each habitat, "indicator species analysis" was conducted (Dufrêne & Legendre, 1997). The indicator values were used to select the most characteristic taxa of each of the habitats. Indicator analyses were performed with the "indval" function implemented in the R package "labdsv."

The variation in the diversity patterns of benthic assemblages (beta diversity) was assessed using multivariate analyses. The beta diversity of the study area was estimated using the Sørensen dissimilarity coefficient (presence/absence data) (Baselga, 2010), as this metric contains all of the necessary properties to assess beta diversity (Legendre & De Cáceres, 2013) and is commonly used. To assess which ecological processes influenced beta diversity patterns (species composition), the beta diversity was partitioned into

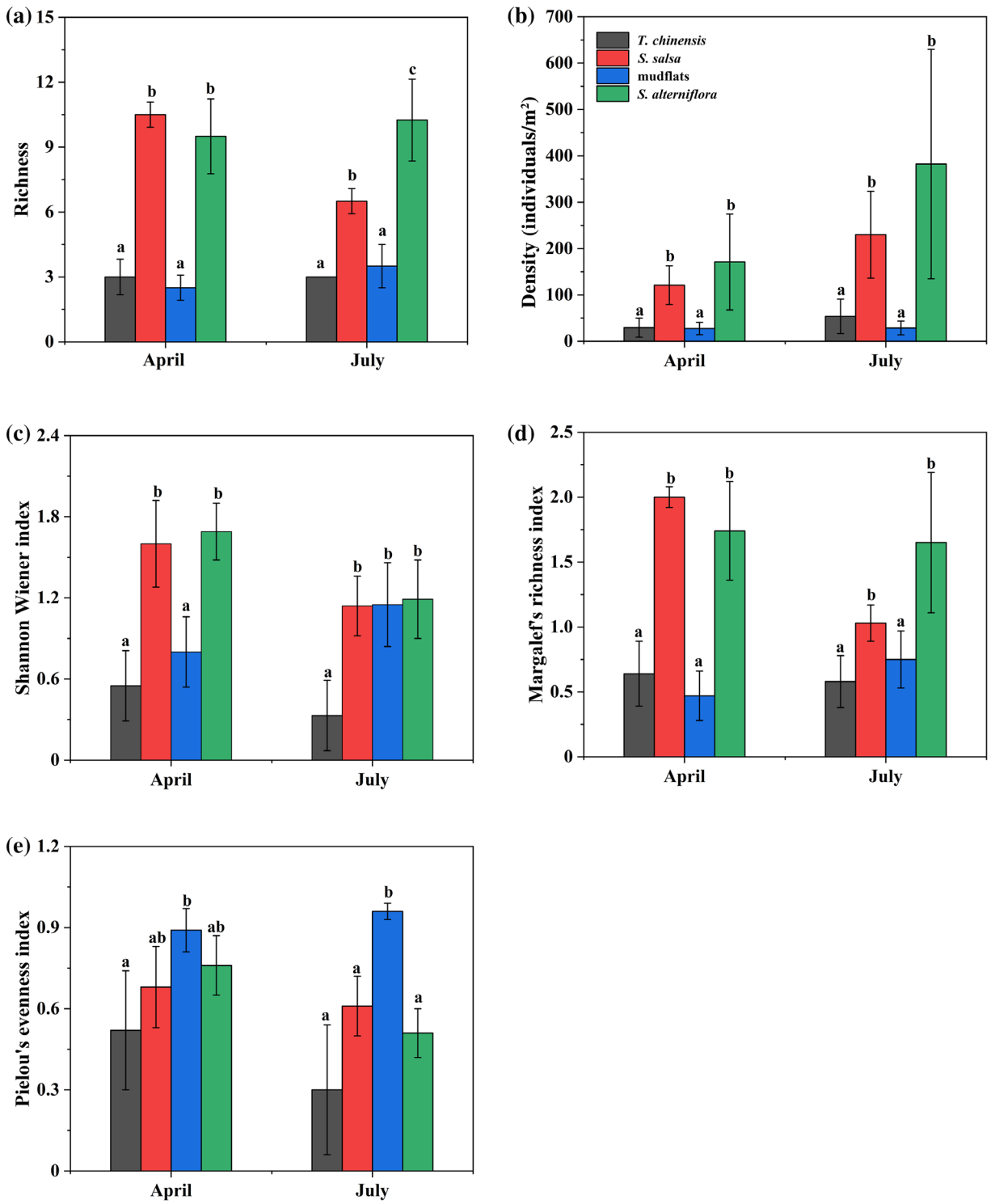


FIGURE 3 Mean of species richness, density (individuals/m^2), and diversity index values of benthic invertebrate assemblages among each habitat in intertidal wetlands of the Yellow River Delta in April and July 2019. Means are plotted with standard deviation, and lowercase letters refer to nonparametric Kruskal–Wallis significant difference tests

replacement and richness differences (Legendre, 2014) or into turnover and nestedness components (Baselga, 2012; Baselga & Leprieur, 2015). The β_{total} value varied from 0 to 1 and corresponds to the sum of β_{repl} and β_{rich}/AbDiffR ($\beta_{total} = \beta_{repl} + \beta_{rich}$/AbDiffR). The closer the β_{total} values, the greater the contribution of replacement or richness/abundance difference to beta diversity. Analyses were conducted in the statistical program R, version 4.0.2 (R Core Development Team, 2020) using the commands "beta.pair" and "beta.multi" of the "betapart" package.

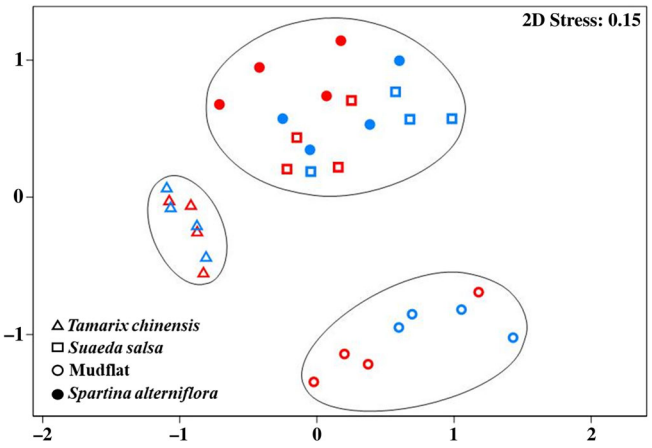


FIGURE 4 Nonmetric multidimensional scaling (NMDS) ordination showing patterns of benthic invertebrate community composition from four different habitats in the intertidal wetlands of the Yellow River Delta in April 2019 (red) and July 2019 (blue). Each point represents the community composition of benthic invertebrates in a single wetland

TABLE 2 Analysis of similarity (ANOSIM) of benthic invertebrate communities among the different habitats using the Bray–Curtis distance measure in the intertidal wetlands of the Yellow River Delta

	ANOSIM pairwise comparison			
	S. salsa and *S. alterniflora*		Mudflat	
Habitat types	***p***	***R***	***p***	***R***
Tamarix chinensis	0.001	0.801	0.001	0.948
S. salsa and *S. alterniflora*	—	—	0.001	0.936

RESULTS

Taxa richness and diversity

A total of 38 benthic invertebrate taxa were enumerated in this study, representing three phyla, 24 orders, and 29 families (Table 1). Of these 38 taxa, almost one-third were only detected within *S. alterniflora* habitats, eight were restricted to *S. salsa* habitat, and only one was unique to *T. chinensis* habitats (Figure 2). Only one species (Malacostraca: *Helice tridens sheni*) was present in all four habitats (Figure 2). Malacostraca (Sergestidae: *Acetes chinensis*) dominated invertebrate assemblages in *T. chinensis* habitats, while Gastropoda dominated the invertebrate assemblages in the *S. salsa* habitats. Polychaeta dominated the mudflat habitats. Gastropoda and Malacostraca were particularly well represented in the *S. alterniflora* habitats.

In April and July, taxon richness was significantly lower in mudflats and habitats containing *T. chinensis* when compared to habitats with *S. salsa* and *S. alterniflora* (Figure 3a; $p < 0.05$). In *S. alterniflora* habitats, the total density of benthic invertebrates was significantly higher than those in native *T. chinensis* and mudflats habitats (Figure 3b; $p < 0.05$); however, it is not statistically significant than that in *S. salsa* habitats.

The Shannon index of invertebrate assemblages in the *T. chinensis* habitats was significantly lower than all other habitats in July (Figure 3c; $p < 0.05$). The Margalef's richness of invertebrate assemblages in *S. alterniflora* habitats was significantly higher than that of assemblages identified in mudflats and *T. chinensis*

TABLE 3 Indicator species analysis among the different habitats in the intertidal wetlands of the Yellow River Delta in April and July 2019

Seasons	Habitat types	Indicator species	Specificity	Fidelity	Indicator value	*p*
April	*Tamarix chinensis*	*Acetes chinensis*	0.728	1	0.728	0.012
	Suaeda salsa	*Stylommatophora*	1	1	1	0.001
		Odostomia subangulata	1	1	1	0.007
		Alvenius ojianus	0.598	1	0.598	0.038
	Spartina alterniflora	*Siliqua pulchella*	1	1	1	0.003
		Stenothyra glabar	0.771	1	0.771	0.006
	Mudflat	—	—	—	—	—
July	*T. chinensis*	*Acetes chinensis*	0.6901	1	0.6901	0.034
	S. salsa	*Stylommatophora*	1	1	1	0.004
		Oncomelania hupensis	1	0.667	0.935	0.002
	S. alterniflora	*Alvenius ojianus*	0.875	1	0.875	0.002
		Stenothyra glabar	0.847	1	0.847	0.01
	Mudflat	—	—	—	—	—

TABLE 4 Beta diversity values of the benthic invertebrate assemblages in both native habitats including *Spartina alterniflora* invasion habitats, decomposed into species turnover and nestedness components

	β_{total}		Turnover		Nestedness	
Habitat types	**April**	**July**	**April**	**July**	**April**	**July**
Native habitats	0.85	0.86	0.7 (82.40%)	0.81 (94.20%)	0.15 (17.60%)	0.05 (5.80%)
S. alterniflora invasion	0.88	0.89	0.78 (88.60%)	0.81 (91.00%)	0.1 (11.40%)	0.08 (9.00%)

habitats (Figure 3d; $p < 0.05$), while no significant differences were found with assemblages in *S. salsa* habitats. The evenness index in mudflat invertebrate assemblages was significantly higher than that in all other habitats in April (Figure 3e; $p < 0.05$).

Structure of benthic invertebrate assemblages

The multivariate analysis identified distinct variations in the structure of benthic invertebrate assemblages. An NMDS plot based on a distance matrix of Bray–Curtis dissimilarity values (stress value = 0.15; Figure 4) identified three main biotopes, including habitats of *S. alterniflora* and *S. salsa*, *T. chinensis*, and mudflat. One-way ANOSIM confirmed the visual interpretation of the NMDS ordinations and revealed significant differences in benthic invertebrate assemblages between the various habitats ($R = 0.88$, $p < 0.05$; Table 2).

SIMPER analysis revealed that the group average similarity of *T. chinensis* was 64.22%, with *Acetes chinensis* representing its characteristic species (contribution rate of 84.70%). The group average similarity of *S. salsa* and *S. alterniflora* habitats was 38.95%, with their characteristic species including *Oncomelania hupensis*, *Alvenius ojianus*, and *Stenothyra glabar* (accumulated contribution rate of 65.00%). The group average similarity of mudflats was 39.86%, with *Macrophthalmus japonicus* and *Glycinde gurjanovae* as its characteristic species (accumulated contribution rate of 59.77%).

Indicator analysis revealed representative taxa for each habitat type in April and July (Table 3). *Acetes chinensis* (Malacostraca: Sergestidae) was an indicator species of *T. chinensis* habitats. Three Gastropoda species (*Stylommatophora*, *Odostomia subangulata*, and *Oncomelania hupensis*) and one Bivalvia species (*Alvenius ojianus*) were indicators of *S. salsa* habitats. Three species, including one Gastropoda species (*Stenothyra glabar*) and two Bivalvia species (*Alvenius ojianus* and *Siliqua pulchella*), were indicators of *S. alterniflora* habitats. No indicator species were identified for the mudflats.

Components of total beta diversity

Values of total beta diversity (β_{total}) between native habitats including *S. alterniflora* habitats were calculated using the Sorensen indices (Table 4). Overall, in April and July, the species turnover component presented greater relative importance in native habitats. After the invasion of *S. alterniflora*, the habitat's beta diversity was slightly increased compared to native habitats. The partition in beta diversity (Table 4) revealed that differences in species composition were generally induced by species turnover and not nestedness; however, invasion of *S. alterniflora* weakened the relative importance of species turnover.

DISCUSSION

Our study identified that an invasion of *S. alterniflora* species increased benthic invertebrate diversity, despite the high hydrological connectivity between the natural intertidal habitat gradients. Native plant (*S. salsa*) habitats act as an interaction zone between tidal and runoff and support high species diversity, representing "biological hotspots" in intertidal wetlands. *S. alterniflora* invasions may drive "biological hotspot" migration of benthic invertebrates and support higher benthic invertebrate diversities than other habitats. Invasion of *S. alterniflora* also increased the beta diversity of the community. The effect of *Spartina* invasions on benthic invertebrates was species-specific, and mollusks were likely under greater influence of plant invasions.

This study identified that the taxa richness, density, and diversity of benthic invertebrate assemblages in *S. alterniflora* habitats were significantly higher than assemblages in other habitats. Complex habitats can support more species than simple habitats, given their greater variety, and quantity of available resources (Pierre & Kovalenko, 2014). The roots and rhizomes of *S. alterniflora* can actively contribute to sediment oxygenation, encouraging faunal colonization (Hedge & Kriwoken, 2000). Therefore, invasions of *S. alterniflora* are likely to provide different microhabitats for benthic invertebrates by altering the native salt marsh habitat structure (Hedge & Kriwoken, 2000). The density of

benthic invertebrates in mudflats was lower than in all other habitats. The mudflat habitats had a low degree of environmental favorableness and, when combined with the physical environmental stresses, may limit the proliferation of benthic invertebrates. In addition, mudflat benthic invertebrate communities suffer a heavy predation pressure by wading birds (Zou et al., 2008). In contrast, the habitat complexity provided by *S. alterniflora* allows the benthic invertebrate protection from abiotic stress or predation, and provides a refuge (Liao et al., 2018; Reis et al., 2019). Invasive plant species have been shown to strongly influence benthic invertebrate communities when invading mudflats by reducing (Vila et al., 2011) or enhancing (Hedge & Kriwoken, 2000; Yan et al., 2020) benthic invertebrate abundance. Our study revealed that the invasive species *S. alterniflora* supports higher benthic community diversity. Our study supports claims that introduced plants can increase species diversity (Davis et al., 2011). Given the vast extent of the *S. alterniflora* invasion in China, the potential consequences of altered benthic invertebrate communities likely have important implications for coastal ecosystem structure and functions, and deserve further attention.

Multivariate analysis revealed distinct differences in benthic invertebrate assemblages among habitat types in intertidal wetlands of YRD. The benthic invertebrate community composition of invasive *S. alterniflora* and native *S. salsa* communities was highly similar, presumably because our sampling site was in an area recently invaded by *Spartina*. However, there were significant differences in both the dominant species and indicator species. Environmental conditions and disturbance regimes modified by plant invasions may favor some invertebrate species while concurrently inhibiting others, depending on species' traits (Cook & Talley, 2014; Talley et al., 2012). We found that *S. alterniflora* resulted in the decreased abundance of gastropods, whereas the Malacostraca were increased. We propose that the effect of *Spartina* invasions on benthic invertebrates is species-specific, with mollusks more likely to be influenced. The extensive root systems of *S. alterniflora* reduce habitat penetrability, making it more difficult for benthic invertebrates, especially mollusks, to form burrows (Kristensen & Kostka, 2005; Wang et al., 2014). In addition, our study found that the four habitats were characterized by different high numbers of taxa, suggesting that the survival of some invertebrate species was highly correlated with habitat properties (Wang et al., 2020).

Based on presence–absence data, the total beta diversities revealed that the species turnover was the most important component in driving beta diversity, while the contribution of nestedness to explaining the benthic invertebrate community variation was lower. Species turnover suggests that the observed community patterns may have resulted from environmental filtering (Sommer et al., 2014). As the environmental conditions of the intertidal wetlands change from the inland to the sea, the number and identity of species that inhabit each habitat zone vary due to environmental filtering owing to salinity, thereby generating a natural species turnover gradient (Medeiros et al., 2020). The mean salinity values of our study ranged from 8.35 to 31.89, revealing a gradient of low-salt to high-salt environments. Different distribution patterns among organisms with varying tolerances of salinity can lead to species turnover (Barnes & Ellwood, 2012; Prado et al., 2014). The presence of salinity gradients also correlates with higher species turnover (Namba et al., 2020). In addition, the high hydrological connectivity of tidal increased the dispersal rates of benthic invertebrates, which caused the significant importance of the turnover component. Invasion of *S. alterniflora* increases the beta diversity of benthic invertebrate communities and the relative importance of species nestedness. The lack of abilities of the benthic invertebrate (e.g., polychaetes and mollusks) to disperse across distant sites (Medeiros et al., 2016), and the connectivity and directionality are of great importance for passive dispersers (Liu et al., 2013). *S. alterniflora* invasion slows down the tidal connectivity and species dispersal, providing a suitable microhabitat and facilitates some species' colonization, resulting in more aggregate communities (Josefson, 2009). This may help explain why the contribution of the species nestedness component was slightly increased.

Further studies are required to evaluate the long-term effects of exotic plant invasions on benthic invertebrate communities, especially to relate these results to aboveground and belowground vegetative biomass metrics. Meanwhile, attention should be focused on the impact of *Spartina alterniflora* invasions on the structure and function of coastal wetland food webs to further our understanding of the potential ecological consequences.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Kangle Lu: Investigation, conceptualization, methodology, writing—original draft, and visualization. Guangxuan Han:

Writing—review and editing. Haitao Wu: Conceptualization, methodology, writing—review and editing, and funding acquisition.

DATA AVAILABILITY STATEMENT

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REFERENCES

Alp, M., and C. Le Pichon. 2020. "Getting from Sea to Nurseries: Considering Tidal Dynamics of Juvenile Habitat Distribution and Connectivity in a Highly Modified Estuarine Riverscape." *Ecosystems* 24: 583–601.

Barnes, R. S. K., and M. D. F. Ellwood. 2012. "Spatial Variation in the Macrobenthic Assemblages of Intertidal Seagrass along the Long Axis of an Estuary." *Estuarine, Coastal and Shelf Science* 112: 173–82.

Baselga, A. 2010. "Partitioning the Turnover and Nestedness Components of Beta Diversity." *Global Ecology and Biogeography* 19: 134–43.

Baselga, A. 2012. "The Relationship between Species Replacement, Dissimilarity Derived from Nestedness, and Nestedness." *Global Ecology and Biogeography* 21: 1223–32.

Baselga, A., and F. Leprieur. 2015. "Comparing Methods to Separate Components of Beta Diversity." *Methods in Ecology and Evolution* 6: 1069–79.

Batzer, D. P., A. S. Shurtleff, and R. B. Rader. 2001. "Sampling Invertebrates in Wetlands." In *Bioassessment and Management of North American Freshwater Wetlands*, edited by R.B. Rader, D.P. Batzer, and S.A. Wissinger, 339–54. New York: John Wiley and Sons.

Bezemer, T. M., J. A. Harvey, and J. T. Cronin. 2014. "Response of Native Insect Communities to Invasive Plants." *Annual Review of Entomology* 59: 119–41.

Blanco, A., A. R. Larrinaga, J. M. Neto, J. Troncoso, G. Mendez, P. Dominguez-Lapido, A. Ovejero, et al. 2021. "Spotting Intruders: Species Distribution Models for Managing Invasive Intertidal Macroalgae." *Journal of Environmental Management* 281: 111861.

Bongiorni, L., F. Nasi, F. Fiorentino, R. Auriemma, F. Rampazzo, M. C. Nordstrom, and D. Berto. 2018. "Contribution of Deltaic Wetland Food Sources to Coastal Macrobenthic Consumers (Po River Delta, North Adriatic Sea)." *Science of the Total Environment* 643: 1373–86.

Carbonell, J. A., J. Velasco, A. Millán, A. J. Green, A. J. Green, C. Coccia, S. Guareschi, and C. Gutierrez-Canovas. 2017. "Biological Invasion Modifies the Co-Occurrence Patterns of Insects along a Stress Gradient." *Functional Ecology* 31: 1957–68.

Castro, D. M. P., M. Callisto, R. R. C. Solar, D. R. Macedo, and G. W. Fernandes. 2019. "Beta Diversity of Aquatic Invertebrates Increases along an Altitudinal Gradient in a Neotropical Mountain." *Biotropica* 51: 399–411.

Chen, H. L., S. Hagerty, S. M. Crotty, and M. D. Bertness. 2016. "Direct and Indirect Trophic Effects of Predator Depletion on Basal Trophic Levels." *Ecology* 97: 338–46.

Clarke, K. R., and R. N. Gorley. 2015. *PRIMER v7 User Manual/Tutorial*. Plymouth: PRIMER-E.

Collinge, S. K., C. Ray, and F. Gerhardt. 2011. "Long-Term Dynamics of Biotic and Abiotic Resistance to Exotic Species Invasion in Restored Vernal Pool Plant Communities." *Ecological Applications* 21: 2105–18.

Cook, R. W., and T. S. Talley. 2014. "The Invertebrate Communities Associated with a *Chrysanthemum coronarium* Invaded Coastal Sage Scrub Area in Southern California." *Biological Invasions* 16: 365–80.

Davis, M., M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, and S. P. Carroll. 2011. "Don't Judge Species on Their Origins." *Nature* 474: 153–4.

Dou, P., T. Xie, S. Z. Li, J. H. Bai, and B. S. Cui. 2020. "A Network Perspective to Evaluate Hydrological Connectivity Effects on Macroinvertebrate Assemblages." *Wetlands* 40: 2837–48.

Dufrêne, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67: 345–66.

Fan, X., B. Pedroli, G. Liu, Q. Liu, H. Liu, and L. Shu. 2012. "Soil Salinity Development in the Yellow River Delta in Relation to Groundwater Dynamics." *Land Degradation and Development* 23: 175–89.

Flood, P. J., A. Duran, M. Barton, A. E. Mercado-Molina, and J. C. Trexler. 2020. "Invasion Impacts on Functions and Services of Aquatic Ecosystems." *Hydrobiologia* 847: 1571–86.

Gao, Z. Q., J. H. Bai, J. Jia, X. J. Wen, G. L. Zhang, and Q. Q. Zhao. 2015. "Spatial and Temporal Changes of Phosphorus in Coastal Wetland Soils as Affected by a Tidal Creek in the Yellow River Estuary, China." *Physics and Chemistry of the Earth* 89–90: 114–20.

Griffiths, M. E., B. A. Mohammad, and A. Vega. 2007. "Dry Season Distribution of Land Crabs, *Gecarcinus quadratus* (Crustacea: Gecarcinidae), in Corcovado National Park, Costa Rica." *Revista de Biologia Tropical* 55: 219–24.

Grosholz, E. 2002. "Ecological and Evolutionary Consequences of Coastal Invasions." *Trends in Ecology & Evolution* 17(1): 22–7.

Hedge, P., and L. K. Kriwoken. 2000. "Evidence for Effects of *Spartina anglica* Invasion on Benthic Macrofauna in Little Swanport Estuary, Tasmania." *Austral Ecology* 25: 150–9.

Jankowski, J. E., A. L. Ciecka, N. Y. Meyer, and K. N. Rabenold. 2009. "Beta Diversity along Environmental Gradients: Implications of Habitat Specialization in Tropical Montane Landscapes." *Journal of Animal Ecology* 78: 315–27.

Josefson, A. B. 2009. "Additive Partitioning of Estuarine Benthic Macroinvertebrate Diversity across Multiple Spatial Scales." *Marine Ecology Progress Series* 396: 283–92.

Kang, C. K., E. J. Choy, S. K. Paik, H. J. Park, K. S. Lee, and S. An. 2007. "Contributions of Primary Organic Matter Sources to Macroinvertebrate Production in an Intertidal Salt Marsh (*Scirpus triqueter*) Ecosystem." *Marine Ecology Progress Series* 334: 131–43.

Kirwan, M. L., and J. P. Megonigal. 2013. "Tidal Wetland Stability in the Face of Human Impacts and Sea-Level Rise." *Nature* 504: 53–60.

Kong, D. X., C. Y. Miao, A. G. L. Borthwick, Q. Y. Duan, H. Liu, Q. H. Sun, A. Z. Ye, Z. H. Di, and W. Gong. 2015. "Evolution of the Yellow River Delta and Its Relationship with Runoff

and Sediment Load from 1983 to 2011." *Journal of Hydrology* 520: 157–67.

Kristensen, E., and J. E. Kostka. 2005. "Macrofaunal Burrows and Irrigation in Marine Sediment: Microbiological and Biogeochemical Interactions." In *Interactions between Macro- and Microorganisms in Marine Sediments*. 125–57. Washington, DC: American Geophysical Union.

Legendre, P. 2014. "Interpreting the Replacement and Richness Difference Components of Beta Diversity." *Global Ecology and Biogeography* 23: 1324–34.

Legendre, P., and M. De Cáceres. 2013. "Beta Diversity as the Variance of Community Data: Dissimilarity Coefficients and Partitioning." *Ecology Letters* 16: 951–63.

Liao, Y. B., L. Shou, Y. B. Tang, A. G. Gao, Q. Z. Chen, X. J. Yan, and J. F. Chen. 2018. "Influence of Two Non-Indigenous Plants on Intertidal Macrobenthic Communities in Ximen Island Special Marine Protected Area, China." *Ecological Engineering* 112: 96–104.

Liu, J., J. Soininen, B. P. Han, and S. A. Declerck. 2013. "Effects of Connectivity, Dispersal Directionality and Functional Traits on the Metacommunity Structure of River Benthic Diatoms." *Journal of Biogeography* 40: 2238–48.

Loke, L. H. L., and P. A. Todd. 2016. "Structural Complexity and Component Type Increase Intertidal Biodiversity Independently of Area." *Ecology* 97: 383–93.

Lu, K. 2021. "Data-Ecosphere-ECS21-0393." https://doi.org/10.5281/zenodo.5739326

McLachlan, J. R., J. M. Haghkerdar, and H. S. Greig. 2019. "Strong Zonation of Benthic Communities across a Tidal Freshwater Height Gradient." *Freshwater Biology* 64: 1284–94.

Medeiros, C. R., J. Heino, P. J. P. dos Santos, J. Molozzi, and R. Ligeiro. 2020. "Spatial Scale Drives Diversity Patterns of Benthic Macroinvertebrate Communities in Tropical Estuaries." *Limnology and Oceanography* 66: 727–39.

Medeiros, C. R., L. U. Hepp, J. Patrício, and J. Molozzi. 2016. "Tropical Estuarine Macrobenthic Communities Are Structured by Turnover Rather than Nestedness." *PLoS One* 11: 1–14.

Namba, M., M. Hashimoto, M. Ito, K. Momota, C. Smith, T. Yorisue, and M. Nakaoka. 2020. "The Effect of Environmental Gradient on Biodiversity and Similarity of Invertebrate Communities in Eelgrass (*Zostera marina*) Beds." *Ecological Research* 35: 61–75.

Noh, J., S. J. Yoon, H. Kim, C. Lee, B. O. Kwon, Y. Lee, S. Hong, J. Kim, J. Ryu, and J. S. Khim. 2019. "Anthropogenic Influences on Benthic Food Web Dynamics by Interrupted Freshwater Discharge in a Closed Geum River Estuary, Korea." *Environment International* 131: 104981.

Pagliosa, P. R., and P. D. C. Lana. 2005. "Impact of Plant Cover Removal on Macrobenthic Community Structure of a Subtropical Salt Marsh." *Bulletin of Marine Science* 77: 1–17.

Pennings, S. C., and M. D. Bertness. 2001. "Salt Marsh Communities." In *Marine Community Ecology*, edited by M.D. Bertness, S.D. Gaines, and M.E. Hay, 313–51. Sunderland: Sinauer Associates.

Petsch, D., F. Schneck, and A. S. Melo. 2017. "Substratum Simplification Reduces Beta Diversity of Stream Algal Communities." *Freshwater Biology* 62: 205–13.

Pierre, J. I. S., and K. E. Kovalenko. 2014. "Effect of Habitat Complexity Attributes on Species Richness." *Ecosphere* 5: 1–10.

Pingram, M. A., K. J. Collier, D. P. Hamilton, B. J. Hicks, and B. O. David. 2014. "Spatial and Temporal Patterns of Carbon Flow in a Temperate, Large River Food Web." *Hydrobiologia* 729: 107–31.

Prado, P., N. Caiola, and C. Ibáñez. 2014. "Freshwater Inflows and Seasonal Forcing Strongly Influence Macrofaunal Assemblages in Mediterranean Coastal Lagoons." *Estuarine, Coastal and Shelf Science* 147: 68–77.

Quan, W. M., H. Zhang, Z. L. Wu, S. F. Jin, F. H. Tang, and J. B. Dong. 2016. "Does Invasion of *Spartina alterniflora* Alter Microhabitats and Benthic Communities of Salt Marshes in Yangtze River Estuary?" *Ecological Engineering* 88: 153–64.

R Core Team. 2020. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Reis, A., M. Krull, L. R. S. Carvalho, and F. Barros. 2019. "Effects of Tropical Saltmarsh Patches on the Structure of Benthic Macrofaunal Assemblages." *Wetlands* 39: 945–54.

Soininen, J., J. Heino, and J. Wang. 2018. "A Meta Analysis of Nestedness and Turnover Components of Beta Diversity across Organisms and Ecosystems." *Global Ecology and Biogeography* 27: 96–109.

Sommer, B., P. L. Harrison, M. Beger, and J. M. Pandolfi. 2014. "Trait-Mediated Environmental Filtering Drives Assembly at Biogeographic Transition Zones." *Ecology* 95: 1000–9.

Talley, T. S., K. C. Nguyen, and A. Nguyen. 2012. "Testing the Effects of an Introduced Palm on a Riparian Invertebrate Community in Southern California." *PLoS One* 7: e42460.

Tonolla, D., V. Acuna, U. Uehlinger, T. Frank, and K. Tockner. 2010. "Thermal Heterogeneity in River Floodplains." *Ecosystems* 13: 727–40.

Vila, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarosik, J. L. Maron, J. U. Pergl, Y. Sun Schaffner, and P. Pysek. 2011. "Ecological Impacts of Invasive Alien Plants: A Meta-Analysis of their Effects on Species, Communities and Ecosystems." *Ecology Letters* 14: 702–8.

Wang, J. Q., M. D. Bertness, B. Li, J. K. Chen, and W. G. Lu. 2015. "Plant Effects on Burrowing Crab Morphology in a Chinese Salt Marsh: Native vs. Exotic Plants." *Ecological Engineering* 74: 376–84.

Wang, M., X. Gao, and W. Wang. 2014. "Differences in Burrow Morphology of Crabs between *Spartina alterniflora* Marsh and Mangrove Habitats." *Ecological Engineering* 69: 213–9.

Wang, S. K., Q. He, Y. Z. Zhang, Q. Sheng, B. Li, and J. H. Wu. 2020. "Habitat-Dependent Impacts of Exotic Plant Invasions on Benthic Food Webs in a Coastal Wetland." *Limnology and Oceanography* 66: 1256–67.

Weilhoefer, C. L. 2011. "A Review of Indicators of Estuarine Tidal Wetland Condition." *Ecological Indicators* 11(2): 514–25.

Wigginton, R. D., J. Pearson, and C. R. Whitcraft. 2014. "Invasive Plant Ecosystem Engineer Facilitates Community and Trophic Level Alteration for Brackish Marsh Invertebrates." *Ecosphere* 5(4): 40.

Wolters, J. W., R. C. M. Verdonschot, J. Schoelynck, P. F. M. Verdonschot, and P. Meire. 2018. "The Role of Macrophyte Structural Complexity and Water Flow Velocity in Determining the Epiphytic Macroinvertebrate Community Composition in a Lowland Stream." *Hydrobiologia* 806: 157–73.

Wu, H. T., Q. Guan, K. L. Lu, G. X. Han, B. Q. Li, and M. Y. Yang. 2020. "Effects of Hydrological Connectivity on Snail Assemblages in the Intertidal Zone of Coastal Wetlands." *Wetlands* 40: 1627–34.

Wu, H. T., M. Y. Yang, K. L. Lu, and D. P. Batzer. 2021. "Effects of Ecological Restoration on Trophic Dynamics in Estuarine Wetlands." *Wetlands* 41: 10.

Yan, J. G., H. C. Sui, H. H. Huang, X. Y. Wang, D. D. Qiu, and B. S. Cui. 2020. "An Integrative Perspective to Understand the Impact of Co-Occurring Ecosystem Engineers on Macroinvertebrates." *Marine Pollution Bulletin* 152: 110921.

Yang, J., Y. Ma, G. Ren, J. Y. Zhang, and Y. G. Fan. 2017. "Monitoring Method of Invasive Vegetation *Spartina alterniflora* in Modern Yellow River Delta Based on GF Remote Sensing Data." *Marine Environmental Science* 36: 596–602.

Yang, M. Y., K. L. Lu, D. P. Batzer, and H. T. Wu. 2019. "Freshwater Release into Estuarine Wetlands Changes the Structure of Benthic Invertebrate Assemblages: A Case Study from the Yellow River Delta." *Science of the Total Environment* 687: 752–8.

Zhang, H., X. Chen, and Y. Luo. 2016. "An Overview of Ecohydrology of the Yellow River Delta Wetland." *Ecohydrology and Hydrobiology* 16: 39–44.

Zou, F. S., H. H. Zhang, T. Dahmer, Q. F. Yang, J. X. Cai, W. Zhang, and C. Y. Liang. 2008. "The Effects of Benthos and Wetland Area on Shorebird Abundance and Species Richness in Coastal Mangrove Wetlands of Leizhou Peninsula, China." *Forest Ecology and Management* 255(11): 3813–8.

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