



Patterns of structural and functional diversity of macrofaunal communities in a subtropical mangrove ecosystem

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ABSTRACT

Biological trait analysis has been successfully used to describe ecological functions in marine benthic ecosystems. However, it has rarely been applied to mangrove habitats. This study analyzes taxonomic and functional diversity and the components thereof in two mangrove habitats in the Hara Biosphere Reserve, Persian Gulf: a vegetated area with both mangrove trees and pneumatophores, and an adjacent mudflat. Species diversity and functional diversity were higher in vegetated habitats and slightly increased in summer. Our study demonstrates the importance of mangrove structural complexity for the structure and functioning of invertebrate communities. The macrofaunal communities were characterized by low diversity and a high dominance of just a few species, such as crab *Opusia indica* which are specifically adapted to this stressed environment. Burrowers, surface deposit feeders, free-living, and large sized organisms were dominant trait modalities that essentially shape the functional composition of arid mangrove ecosystem of the Persian Gulf. The low functional redundancy among species implies that small changes in species diversity may have marked impacts on the system functional diversity.

1. Introduction

Mangroves are important ecosystems along tropical and subtropical coasts that support a variety of ecological services (Adame et al., 2020; Bouillon et al., 2002). Mangroves provide spawning, nursery and feeding grounds for marine fauna (Nordhaus et al., 2019; zu Ermgassen et al., 2020), protect coastal areas from storm and sea level rise (Alongi, 2012) and recycle nutrients through various biogeochemical processes (Mattone and Sheaves, 2017; Nordhaus et al., 2017). Mangroves mitigate climate change by sequestering and storing significant amounts of carbon in living biomass and sediments (McLeod et al., 2011; Soper et al., 2019). The carbon trapped in mangrove sediments, can be stored for decades or even millennia, as anoxic water-logged sediments delay the decomposition of organic matter (Jennerjahn et al., 2017; Murdiyarso et al., 2015). Mangroves are threatened by natural and anthropogenic disturbances, including changed hydrodynamic, subsidence, industrial pollutants, clearcutting and climate variability (Adame et al., 2020; Jennerjahn, 2020). Although many countries have deployed conservation measures, mangrove forests are declining at a global rate of approximately 0.2% per year (Atwood et al., 2017; Richards et al., 2020).

The benthic macrofaunal communities are ecologically important components of mangrove ecosystems. They link primary producers with higher trophic levels (Janas et al., 2019), facilitate the decomposition of organic matter (Wrede et al., 2018) and increase the flux of oxygenated seawater into sediments through burrowing activity (Nordhaus et al., 2019). Mangrove degradation and the associated reduction in habitat complexity have adverse effects on biodiversity and ecological functioning of benthic communities (Bouillon et al., 2002). Because of their limited mobility, benthic organisms cannot escape from deteriorating conditions and may, thus, be particularly sensitive to environmental disturbance. (Gutow et al., 2020; Nordhaus et al., 2009; Shojaei et al., 2016).

Classically, biodiversity is measured in terms of the taxonomic composition of communities and the abundance and distribution of individuals among the constituting species. Alternatively, 'functional diversity', is increasingly being investigated to understand the responses of ecosystems to environmental fluctuations (Torca et al., 2019; Törnroos et al., 2013; van der Linden et al., 2017), which is the diversity of functional traits (e.g., feeding habit, body size, mobility) occurring among sets of species in a given ecosystem (Wong and Dowd, 2015). Traits are morphological, physiological and behavioral characteristics

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that define how species interact with the environment, with conspecifics, and with individuals of other species (Bremner et al., 2006; Degen et al., 2018; Nordström et al., 2015; Teichert et al., 2017). Several approaches are used to characterize functional trait composition and diversity across communities. Biological Trait Analysis (BTA) is a useful approach recently proposed for describing ecological functioning of terrestrial and marine ecosystems. BTA was first applied in studies on terrestrial plants (McIntyre et al., 1995) and freshwater organisms (Dolédec et al., 1996). Over the past decade this approach has progressively been applied to marine benthic communities (Henseler et al., 2019; Törnroos et al., 2013). BTA combines structural data (i.e., species abundance or biomass) with information on functional features of the species to characterize the ecological functioning of an ecosystem (Bremner et al., 2006; Shojaei et al., 2015). Phylogenetically related and unrelated species can evolve similar adaptations and functions in response to environmental constraints. Therefore BTA allows for comparing ecological functioning between communities, regardless of taxonomic composition (Beauchard et al., 2017; Ruhí et al., 2013).

Research on biodiversity-ecosystem functioning (BEF) has received increasing attention over the last two decades, with a successful application of trait-based approaches (Gamfeldt et al., 2014; Hooper et al., 2005). Theoretical studies suggest that the relationship between species and functional diversity will differ between systems, depending on the number of the species and their functional traits (Hewitt et al., 2008; Micheli and Halpern, 2005). The number of species equally contributing to an ecosystem function describes the potential for functional redundancy and determines how the loss of species alters ecological functioning (Teichert et al., 2017; van der Linden et al., 2017). Ecosystems with high redundancy are assumed to be resistant against disturbance, resilient, and stable (Guillemot et al., 2011; Hewitt et al., 2008; Naeem et al., 2002). Species diversity does not always correlate with functional diversity. Therefore, determining the relationship between species diversity and functional diversity is central for predicting the consequences of change in the species inventory for ecosystem functioning (Micheli and Halpern, 2005; Wong and Dowd, 2015). Here, we use data on the macrofauna of a mangrove ecosystem in the Persian Gulf to

examine the relationship between species diversity and functional diversity. Mangrove benthic communities are reasonably well characterized with regards to species diversity, biomass, relative abundance, and trophic structure (Alfaro, 2006; Freitas and Pagliosa, 2020; Nordhaus et al., 2009; Sheridan, 1997). However, studies on functional diversity and composition of macrofauna in mangroves are as scarce (Freitas and Pagliosa, 2020; Leung and Cheung, 2017). The objective of our study was to compare the taxonomic and functional composition and diversity of macrofaunal communities in an arid mangrove system on the northern coast of the Persian Gulf. More specifically, we assessed (1) how taxonomic and functional diversity vary between two different mangrove habitats, namely a vegetated area vs. a mudflat and (2) which species and functional traits are responsible for between-habitat differences.

2. Material and methods

2.1. Study area

The study was carried out at the Hara Biosphere Reserve on the northern coast of the Persian Gulf (Fig. 1). This area represents the largest mangrove forest of the Persian Gulf, with an area of about 58 km², contributing 70% to the mangrove coverage in that region. The mangrove forest composed of mostly monospecific stands of *Avicennia marina*, with scattered small patches of planted *Rhizophora mucronata*, which cover a total area of only 1 km². The climate in the area is arid, with a mean annual air temperature of 26.9 °C (7–46 °C) and rainfall of <200 mm yr⁻¹ (Sheppard et al., 2010). There are no major freshwater discharges into the forest (except two seasonal rivers), and tidal water exchange with the open sea occurs through the Khuran Channel (Shahraki et al., 2014). The tide is semidiurnal, with a tidal range of 1–3 m at neap tides and 3–4 m at spring tides (Reynolds, 2002). In summer evaporation (1000–2000 mm) exceeds precipitation due to high temperatures and dry winds, increasing salinities to >39 PSU (Sheppard et al., 2010). The study site is listed in the Ramsar Convention for wetland protection and was recognized a biosphere reserve in 1977 by

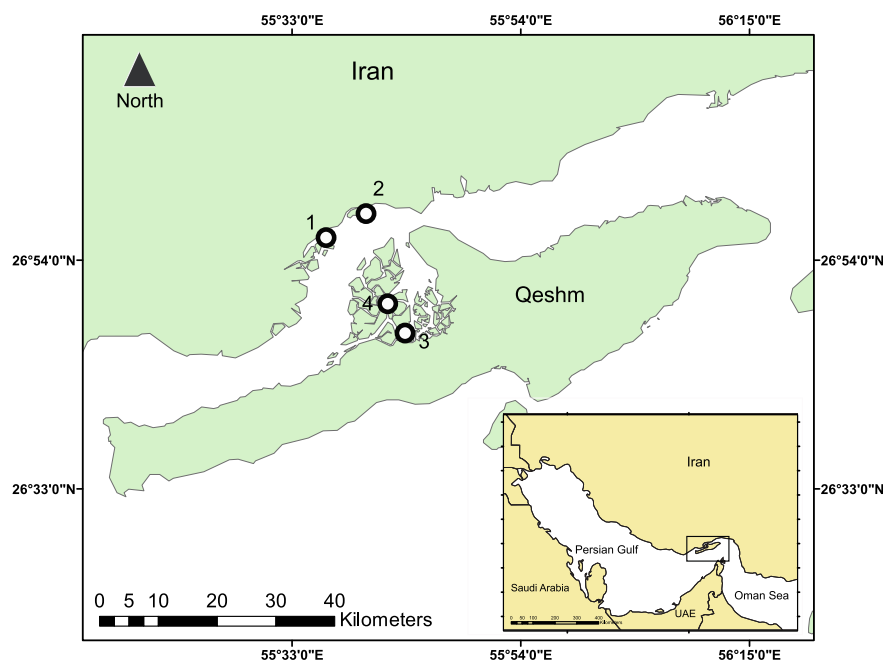


Fig. 1. Positions of the four sampling sites of macrofauna in the Hara Biosphere Reserve, Persian Gulf.

the Coordination Council of the Man and Biosphere Program (MaB) of UNESCO.

2.2. Sampling of macrofauna

Sampling was performed in January and July 2018 at four study sites in natural mangrove forests of the Persian Gulf. January is the coldest month of the year with an average monthly air temperature of 18.1 °C, whereas July is the warmest month of the year with an average temperature of 34.5 °C (Mafi-Gholami et al., 2017). The mangrove ecosystem in the study area comprises two structurally different habitat types: *vegetated* and *mudflat*. The vegetated habitat was dominated by mangrove trees and dense pneumatophores. The mudflat was defined by the absence of trees as well as pneumatophores and located immediately seaward of the vegetated habitat. In each habitat, one random plot was centered at least 8 m from the forest fringe in order to avoid edge effects potentially affecting the community composition. Three random sediment samples were taken at each plot using a metal 25 cm × 25 cm quadrat, down to a depth of 20 cm. The sediment samples were washed through a 500 µm sieve, and the retrieved organisms were preserved in 70% Ethanol until further processing. In the laboratory, all organisms were identified to the lowest taxonomic level possible and the number of individuals was counted for each species.

2.3. Environmental data

Five environmental variables were selected, which are known to influence the composition of benthic communities (Beseres Pollack et al., 2011; Franke and Gutow, 2004). The variables included temperature (°C), salinity (PSU), total organic carbon (TOC), total organic nitrogen (TON), and sediment grain size. During the collection of the sediment samples, salinity, and temperature were measured in situ using a portable device that had been recently calibrated. For the determination of the sediment geochemistry, three replicate samples were taken from each plot using sampling cores (internal diameter: 5 cm, depth: 10 cm). The sediment samples were taken in immediate vicinity of the macrofauna samples. The cores were sectioned in layers of 5–10 mm and dried in the open air in the shade. At each plot, an additional core was taken for sediment granulometry. Percentages of sand, silt, and clay were determined following the Bouyoucos hydrometer method (Bouyoucos, 1962). Total organic carbon (TOC) of the sediment samples was determined using the modified Walkley-Black technique (Allison, 1975) and total organic nitrogen (TON) using a semi Micro-Kjeldahl technique (Bremner and Mulvaney, 1983). An environmental data matrix, including sediment composition (% silt/clay, percentage of TOC, and percentage of TON), temperature, and salinity were transformed (log x+1) and normalized prior to analyses (Clarke and Gorley, 2006).

2.4. Trait data

A set of seven biological traits was selected describing life history, behavioral characteristics, morphological attributes and environmental preferences of benthic species. Traits were divided into *a priori* defined modalities derived from the characteristics of the taxa involved (Table 1).

Species can shift between modalities depending on the environmental conditions and resource availability (Usseglio-polatera et al., 2000). Therefore, a ‘fuzzy scoring’ approach (Chevene et al., 1994) was applied to assign a score between 0 and 3 to each modality according to the affinity of a taxon to a specific trait modality (0 = no affinity, 1 and 2 = partial affinity, and 3 = highest exclusive affinity). For example, the crab *Eurycarcinus orientalis* mostly feeds as a predator/scavenger but may occasionally feed as a detritivore. Accordingly, the species was coded 3 for ‘predator’ and 1 for ‘detritivore’ for the trait ‘feeding habit’. Information on traits was compiled from identification guides, peer-reviewed literature, online databases (e.g. <http://www.marlin.ac.uk/biotic/>) and personal expert consultations. If trait information was not available at the species level, the information was inferred from the genus or the family level. The full data on the species traits with an attributed reference list are available in the supplementary material, Table S1. The frequency of each trait modality in the data set was calculated by weighting the modality scores by the abundance of each species exhibiting that modality. This resulted in a sample by trait matrix showing the abundance of biological traits for each habitat/time combination (for details see Bremner et al., 2006).

Table 1

Biological traits and trait modalities of macrofauna species used in the biological trait analysis. A label is given for each category.

Traits	Modalities	Labels
Feeding type	Surface Deposit feeder	FDSF
	Sub-surface Deposit Feeder	FSSS
	Suspension/Filter Feeder	FDSF
	Detritivore	FDDE
	Predator/Scavenger	FDPS
	Grazer/Scraper	FDGS
Living habit	Burrow dweller	AHBD
	Free living	AHFL
	Tubicolous	AHTU
Larval development	Direct development	LDDD
	Lecithotrophic	LDLE
	Planktotrophic	LDPL
Size of organism (mm)	0 < 5	SO < 5
	5–10	SO10
	10–50	SO50
	50–100	SO100
Adult movement	Sessile	AMSE
	Burrower	AMBU
	Crawler	AMCR
	Swimmer	AMSW
Life span (year)	0 < 1	LS < 1
	1–2	LS2
	2–10	LS10
Flexibility	High	FLHI
	Intermediate	FLIN
	Low	FLLO
	None	FLNO
Migration	Non-migratory	MINM
	Vertical	MIVE
	Horizontal	MIHO

<http://www.marlin.ac.uk/biotic/>) and personal expert consultations. If trait information was not available at the species level, the information was inferred from the genus or the family level. The full data on the species traits with an attributed reference list are available in the supplementary material, Table S1. The frequency of each trait modality in the data set was calculated by weighting the modality scores by the abundance of each species exhibiting that modality. This resulted in a sample by trait matrix showing the abundance of biological traits for each habitat/time combination (for details see Bremner et al., 2006).

2.5. Data analysis

For multivariate analysis, the species abundance and abundance-weighted-trait data were $\ln(x+1)$ transformed to balance the importance of common and rare taxa and traits. The similarity between samples was calculated using the Bray–Curtis coefficient (PRIMER v7; Clarke and Gorley, 2006).

The patterns of species and trait composition were visualized using Principal Coordinate Analysis (PCO). A repeated measure PERMANOVA model (permutational multivariate analysis of variance) with ‘habitat’ and ‘season’ as fixed factors was conducted to test for effects of habitat and season and their interaction. In cases where the species and trait composition differed significantly, a similarity percentages procedure (SIMPER) with a 90% accumulative contribution cut-off was used to highlight the species and trait modalities, which contributed most to the observed differences. The similarity matrices of environmental variables were calculated as the normalized Euclidean distance. Distance-based Linear Modeling (DISTLM) was used to determine how much of the variation in species and trait composition was attributable to the environmental variables. The Akaike Information Criterion (AIC) was used to establish the selection criteria, on the basis of the best selection procedure, to enable the fitting of the best explanatory environmental variables in the model (Anderson et al., 2008). A distance-based redundancy analysis (dbRDA) was then used to perform an ordination of fitted values from the given model built by the DISTLM routine.

Before running the DISTLM and dbRDA routines, multi-collinearity among environmental variables was examined using Spearmanrank correlation coefficients. All variables were tested because no collinearity was detected. The analyses were performed using the PRIMER v6 statistical package (Clarke and Gorley, 2006), together with the PERMANOVA + PRIMER add-on package (Anderson et al., 2008). In addition to the multivariate community analysis, we calculated species richness, Shannon–Wiener diversity $H'(\log_e)$ and Pielou's evenness, each representing different aspects of biodiversity. Functional diversity was measured as Rao's quadratic entropy (Q) (Rao, 1982). Analyses were performed in R using the packages 'ade-4', 'tcltk' and 'vegan' (R Development Core Team, 2011). A Mann-Whitney U test and a paired sample Wilcoxon test were used to evaluate differences in diversity indices between habitats and between seasons. The univariate analyses were performed using the SPSS 16 software package. The level of functional redundancy was explored from the shape of the relationship between species and functional diversity (Micheli and Halpern, 2005; Teichert et al., 2017). A linear relationship suggests that each increase in

species diversity is followed by an increase in functional diversity, implying low functional redundancy as each new species adds new traits (Naeem et al., 2002; Teichert et al., 2017). In contrast, a curvilinear association would indicate that at some level of species diversity, functional diversity does not increase because the functional traits are shared among an increasing number of species (Floyd et al., 2020; Teichert et al., 2017). The overall degree of functional redundancy was assessed from the relationship between species diversity and Rao's index (Teichert et al., 2017). The relationship was tested by linear regression analysis (significance level: $P = 0.05$) which provided the best model fit. To provide further support for the regression analysis, functional redundancy was calculated as the ratio between Rao's index and Shannon–Wiener diversity (van der Linden et al., 2012), which increases with decreasing functional redundancy and vice versa.

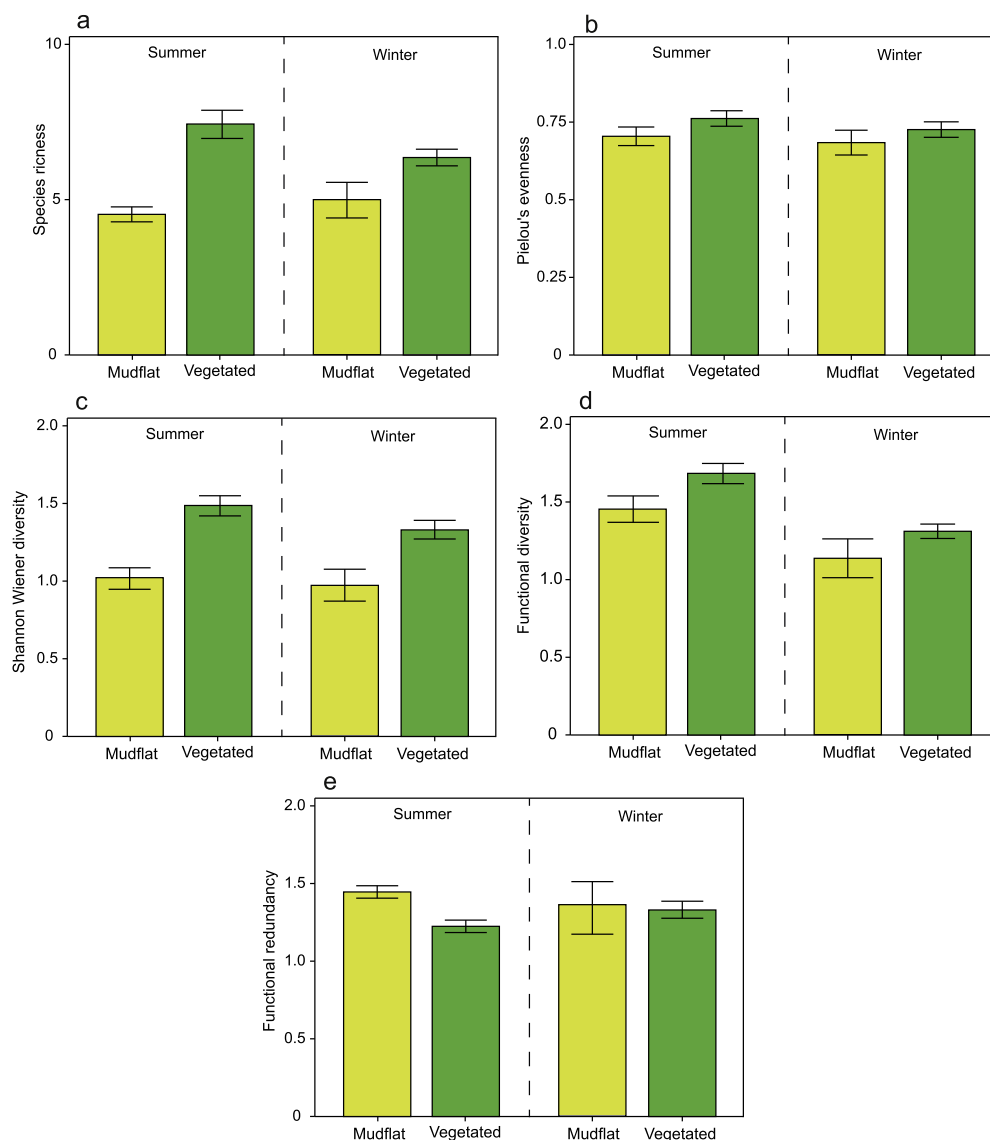


Fig. 2. Diversity indices of the benthic macrofauna communities in vegetated and un-vegetated habitats of a mangrove ecosystem in the Persian Gulf in summer and winter; (a) species richness, (b) Pielou's evenness, (c) Shannon–Wiener index, (d) Rao's index and (e) functional redundancy. Error bars show standard errors.

3. Results

3.1. Structural and functional diversity of macrofaunal communities

A total of 18048 individuals from 45 taxa of macrofauna were found at the Hara Biosphere Reserve. Crustaceans were most abundant ($N = 10264$ individuals), followed by polychaetes ($N = 4288$ individuals) and gastropods ($N = 3120$ individuals). The most abundant crustacean families were Camptandriidae, (two species: *Opusia indica* and *Manningis arabicum*), Sesamidae (one species: *Parasesarma persicum*) and Pilumnidae (one species: *Eurycarcinus orientalis*). The most abundant polychaete families were Capitellidae and Nereididae, the latter being represented mostly by *Perinereis horsti* and *Simplisetia qeshmensis*. The most abundant gastropod families were the Potamididae represented by *Pirenella cingulata*; Assimineidae represented by *Assimineia* sp. and Onchidiidae represented by *Plateindex tigrinus*. In addition, bivalves (mostly *Barbatia trapezina*) were found (Supplementary material; Table S2).

All diversity metrics had higher mean values in the vegetated habitats than on the adjacent mudflat (Fig. 2). Pielou's evenness index did not differ significantly between habitats in either season. Species richness and the Shannon–Wiener diversity were higher in vegetated habitats in summer (Fig. 2a–c) (Mann–Whitney $U_{\text{Richness}} = 29$, $p = 0.012$; Mann–Whitney $U_{\text{Shannon–Wiener}} = 34$, $p = 0.042$). Both indices did not differ significantly between habitats in winter, although their mean values were slightly higher in vegetated habitats than in mudflats. Rao's index and functional redundancy index did not differ between habitats in winter, while in summer, Rao's index was higher in vegetated habitats than on mudflats (Fig. 2d; Mann–Whitney $U_{\text{Rao's index}} = 53$, $p = 0.029$). None of the diversity indices differed significantly between summer and winter in either habitat, even though only Rao's index in vegetated habitats was significantly higher in summer than in winter ($Z_{\text{Rao's index}} = -1.511$, $p = 0.049$). There was a significant positive relationship between Shannon–Wiener diversity and Rao's index ($R^2 = 0.49$, $p < 0.01$, $df = 45$, Fig. 3). A linear model explained the variability best indicating low functional redundancy within the benthic communities. The repeated measures PERMANOVA test for effects of 'habitat' and 'season' revealed that both factors significantly affected the species composition (habitat: $F = 3.31$, $p = 0.0007$; season: $F = 2.73$, $p = 0.0034$) and trait composition (habitat: $F = 2.57$, $p = 0.0391$; season: $F = 10.69$, $p = 0.0001$). However, there was no significant interaction between 'habitat' and 'season' (Table 2). PCO analysis graphically revealed clear separation of species and trait composition between habitats and seasons (Fig. 4). In addition, the PCO ordination showed that the first two components accounted for 34.5% (PCO1, 20.1% and PCO2, 14.5%) of the variability in species composition and 63.6% (PCO1, 46.1% and PCO2, 17.5%) of

the variability in trait composition (Fig. 4). SIMPER analysis based on the species abundance data revealed that the dissimilarity between habitats (79.32% average dissimilarity) was mainly due to the Capitellidae (contribution: 9.82%), *Opusia indica* (contribution: 9.34%), *Perinereis horsti* (contribution: 6.88%), and *Manningis arabicum* (contribution: 6.65%). An average dissimilarity of 78.25% was detected between seasons, which was mostly explained by *O. indica* (contribution: 9.67%), Capitellidae (contribution: 8.01%), *M. arabicum* (contribution: 6.91%) and *P. horsti* (contribution: 6.32%). SIMPER analysis based on trait composition revealed the dissimilarity of 34.75% between habitats, which was mainly due to the modalities high flexibility (contribution: 5.77%) and surface deposit feeder (contribution: 5.36%). The dissimilarity between seasons (32.30% average dissimilarity) was mainly attributed to the modalities planktotrophic larval development (contribution: 9.12%) and crawler (contribution: 5.05%). The abundance-weighted means of trait modalities were plotted to visualize a trait composition for each habitat and season (Fig. 5). The dominating trait modalities in the macrofaunal communities of the mangrove ecosystem were burrower, surface deposit feeder, free-living, planktotrophic larval development, medium life span, and large size.

3.2. Environmental variables

Five environmental variables (Table 3) were used to build the best DISTLM model, applied to both species and trait composition. Regarding species composition, the marginal test revealed that temperature and salinity each explained the variation in species composition ($p < 0.05$; Table 4). The best model was achieved by a combination of the silt to clay ratio, temperature, and salinity, which accounted for 15.9% of the variability of the data ($R^2 = 0.159$, AIC = 353.86; Table S3). For the trait composition, only temperature was statistically significant as identified by the marginal test ($p < 0.05$; Table 4), while the best model was built upon the combination of silt to clay ratio, temperature, and salinity which accounted for 22.9% of the variation ($R^2 = 0.229$, AIC = 278.07; Table S3). In the dbRDA performed on species data, the first two axes explained 86.3% of the total variation (dbRDA1 = 59.4%; dbRDA2 = 26.9%) (Fig. 6a). The temperature and salinity were the major contributors of the first factor (dbRDA loading = 0.873 and -0.483 , respectively), whereas the major contributor of the second factor was the silt to clay ratio (dbRDA loading = -0.966). The first two dbRDA axes explained 93.6% of the variability of the fitted model on the trait data (dbRDA1 = 65.5%; dbRDA2 = 28.1%) (Fig. 6b). Temperature was the major contributor of the first factor (dbRDA loading = 0.978), whereas the major contributors of the second axis were salinity and the silt to clay ratio (dbRDA loading = -0.831 and -0.544 , respectively).

4. Discussion

A distinct community composition, both taxonomically and functionally, was found for benthic invertebrates in vegetated and un-vegetated habitats, suggesting differences in ecological functioning between the habitats (Taupp and Wetzel, 2019). Burrower, surface deposit feeder, free-living, and large size were the dominant trait modalities demonstrating the importance of these modalities in shaping the functional composition of macrofaunal communities in mangrove ecosystems. The vegetated habitats supported relatively higher species and functional diversity than the un-vegetated habitats. The structural complexity of mangrove forests is assumed to provide more food sources and shelter than un-vegetated mudflats and to attract organisms from nearby habitats with potential positive effects on local biodiversity (Agusto et al., 2020; Hickey et al., 2018). For instance, pneumatophores provide microhabitats, reduce predation through the provision of refuges for prey organisms, and promote sediment oxygenation, resulting in the colonization by macrofaunal species (Kristensen et al., 2010; Leung, 2015; Nordhaus et al., 2017). Furthermore, trunks and pneumatophores act as a barrier, reducing current velocity and wave energy.

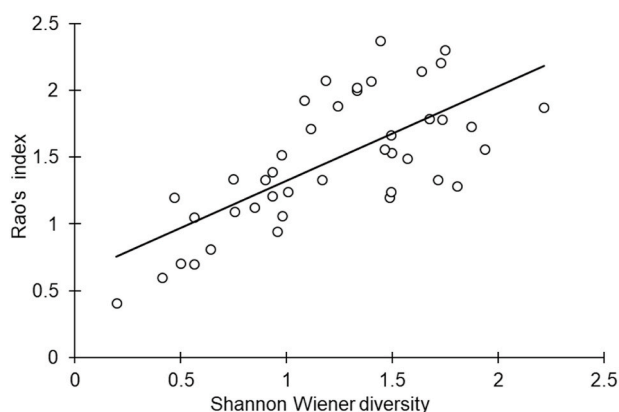


Fig. 3. Relationship between Shannon–Wiener diversity and Rao's index ($y = 0.708x + 0.616$) of the benthic macrofauna in a mangrove ecosystem in the Persian Gulf. Each point represents the diversity value at each sampling site.

Table 2

Results of PERMANOVA for comparing species and trait composition of the benthic macrofauna across habitats and seasons in a mangrove ecosystem in the Persian Gulf. Factors: habitat (levels: vegetated and mudflat) and season (levels: winter and summer).

Source	Species composition				Trait composition			
	df	MS	Pseudo-F	P-value	df	MS	Pseudo-F	P value
Habitat	1	9448.7	3.319	0.0007	1	1257	2.5716	0.0391
Season	1	7799.7	2.7397	0.0034	1	5225.6	10.69	0.0001
Habitat × Season	1	1699.8	0.59708	0.8152	1	926.47	1.8954	0.1016
Residual	40	2846.9			40	488.81		
Total	43				43			

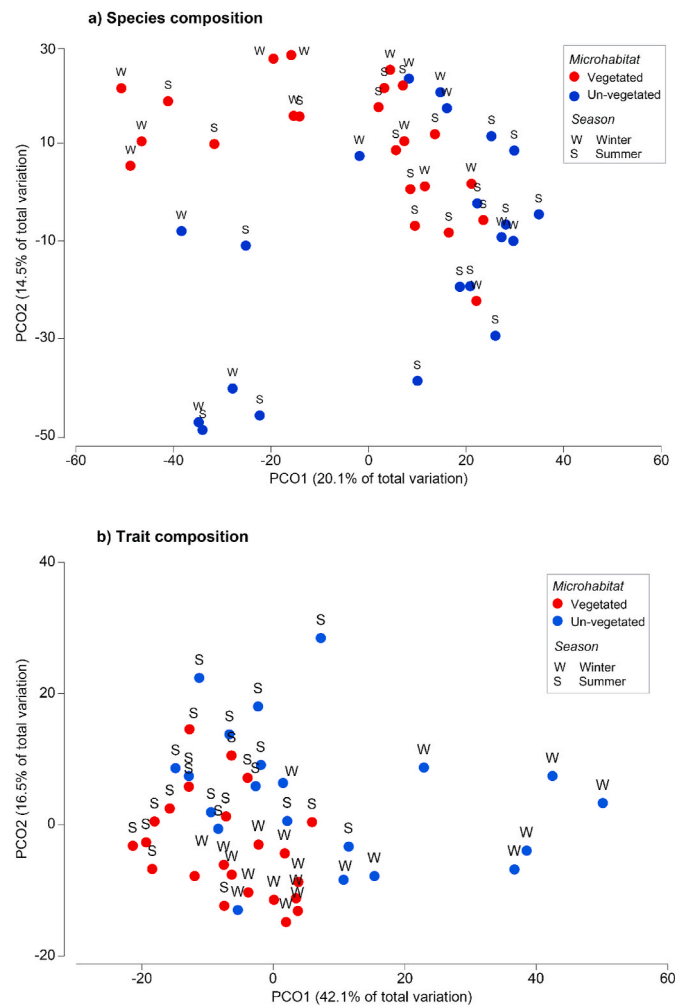


Fig. 4. The principal coordinate analysis (PCO) of macrofaunal (a) species composition and (b) trait composition in vegetated and un-vegetated habitats of a mangrove ecosystem in the Persian Gulf. PCO1 and PCO2 are the first and the second principal coordinates, respectively. The proportion of variance explained by the principal coordinates is given in parentheses.

This favors the settlement of larvae and the deposition of sediments and organic matter, which provides food for resident species (Sahoo et al., 2018). In the harsh environment of the Persian Gulf, shading by the mangrove canopy forms a stable physical environment, with reduced temperature fluctuations and elevated sediment moisture (Adame et al., 2020; Bouillon et al., 2002; Nordhaus et al., 2019). Previous studies reported contradictory results from comparisons of macrofaunal communities between mangrove and adjacent un-vegetated habitats (Alfaro, 2006; Ellis et al., 2004; Leung, 2015; Sheridan, 1997). For example, Alfaro (2006) reported that mangroves have the lowest diversity and density among the six habitats at Matapouri Estuary, New Zealand,

whereas Sheridan (1997) found higher macrofaunal densities in mangroves compared to adjacent un-vegetated habitats in Rookery Bay, Florida. These differences may be the result of different sampling periods and methodologies applied in the two studies (Alfaro, 2006; Sheridan, 1997). Mangroves along the Persian Gulf coast thrive in an arid environment, with high seawater temperatures and salinity. Salinity may be a limiting factor, restricting both abundance and diversity of macrofauna communities (van der Wal et al., 2017). High salinity levels can also result in physiological stress to mangrove trees, forcing them to allocate more energy to osmotic regulation at the expense of growth (Ball, 2002) potentially affecting mangrove net primary productivity and the diversity of the associated macrofauna (Ball, 2002; Chowdhury et al., 2019). The low species richness of the macrofauna may also be attributed to low mangrove tree diversity. *Avicennia marina* is the only species of mangrove in the Persian Gulf, due to its tolerance towards high salinity and extreme temperatures (Adame et al., 2020; Amir and Duke, 2019). Mangrove systems with a low number of mangrove tree species have reduced structural complexity and primary production, which affects the diversity of the associated fauna (Nordhaus et al., 2009).

Functional diversity is a key component of biodiversity with essential implications for ecosystem functioning and sustainability (Breine et al., 2018; Degen et al., 2018). Ecosystems with high functional diversity operate more efficiently (McGovern et al., 2020) and are more resilient to environmental changes (Naeem et al., 2002). However, patterns in the relationship between functional diversity and resilience of ecosystems are inconsistent (Cadotte et al., 2011; Craven et al., 2018). In the Hara Biosphere Reserve mangrove, vegetated habitats harbored higher macrofaunal functional diversity than un-vegetated habitats. A similar relationship has been observed for functional trait measures in coastal vegetated habitats (Henseler et al., 2019; Milesi et al., 2016; Törnroos et al., 2013). For example, seagrass meadows have a higher taxonomic and functional diversity of the benthic macrofauna than bare sand and rocky reef habitats (Henseler et al., 2019). Similarly, the taxonomic and functional diversity differed between habitats (bare sand, seagrass above- and belowground, canopy-forming algae), with highest values found in the seagrass aboveground habitat (Törnroos et al., 2013). The result of the current study showed that, in winter, the type of habitat had only little effect on the taxonomic and functional structure of the communities in the mangrove system. These results are surprising because species diversity and composition of macrofaunal communities can vary between different small-scale habitat structures (Boström et al., 2010; Leung, 2015) and the functional structure of communities can shift at the transition from one habitat to another (Guillemot et al., 2011; Micheli and Halpern, 2005).

In the current study, each habitat displayed a characteristic community composition, with distinct species and trait community compositions for vegetated and adjacent un-vegetated habitats. Differences in taxonomic composition between habitats are known for coastal systems, for instance, for intertidal mudflats and mangrove habitats along the northern coast of New Zealand (Ellis et al., 2004) and between mangroves, seagrass beds and un-vegetated mudflats in Rookery Bay, Florida (Sheridan, 1997). Similarly, species and trait composition differ between mangrove habitats in Tai, Honk Kong (Leung, 2015) suggesting

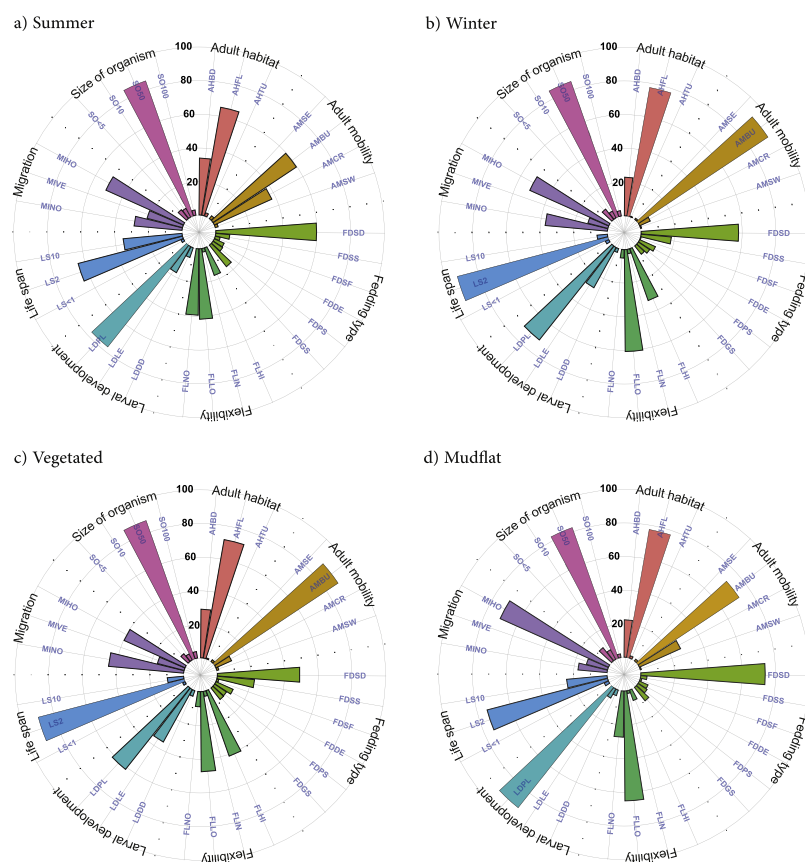


Fig. 5. Abundance-weighted means of trait modalities of the benthic macrofauna from different habitats and seasons in a mangrove ecosystem in the Persian Gulf. Color codes represent the trait affiliation; individual bars represent the trait modality expression. For trait modalities labels see Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Variations in environmental data (mean \pm SD) between habitats and seasons in a mangrove ecosystem in the Persian Gulf. (TOC = Total Organic Carbon; TON = Total Organic Nitrogen).

Season	Summer		Winter	
	Vegetated	Mudflat	Vegetated	Mudflat
Temperature ($^{\circ}$ C)	32.63 \pm 1.12	31.55 \pm 1.68	24.38 \pm 1.07	24.98 \pm 1.88
Salinity (PPT)	31.58 \pm 1.12	31.08 \pm 1.10	31.43 \pm 0.79	31.19 \pm 0.81
TOC	0.77 \pm 0.22	0.47 \pm 0.12	0.68 \pm 0.35	0.64 \pm 0.42
TON	0.05 \pm 0.01	0.04 \pm 0.003	0.22 \pm 0.36	0.06 \pm 0.03
Silt/clay (%)	1.25 \pm 0.54	1.77 \pm 1.19	1.27 \pm 0.56	1.71 \pm 1.12

that taxonomic and trait composition of macrofauna communities depend on the structural complexity of the respective habitat (Henseler et al., 2019).

The relationship between functional traits and ecosystem functions is complex. A specific function may depend on a single trait state.

However, this is not always the case and often functions may be correlated with numerous traits within and among states (Bellwood et al., 2019; Siqueira et al., 2019). In our study, surface deposit feeding prevailed in both habitats, suggesting the relative importance of sediment mixing, particle burial and transport by benthic fauna in mangrove ecosystems. Free living and burrowing prevailed in both habitats, suggesting intense sediment oxygenation and nutrient cycling from the activities of benthic invertebrates. Additionally, large animals may further enhance sediment oxygenation and nutrient cycling. The link between functional traits and ecosystem functions has been investigated experimentally. However, this would be difficult in large-scale studies (Bolam and Eggleton, 2014; Wong and Dowd, 2015). For example, Wrede et al. (2018) demonstrated that burrow type and feeding habit are important for biogeochemical cycling in marine sediments. Similarly, oxygen and nutrient flux across the sediment-water interface is related to body size trait (Norkko et al., 2013). However, even in the absence of data from direct measurements, knowledge of functional diversity and functional trait composition can provide useful insight into ecosystem functioning. Studies on functional diversity are particularly important for quantitative comparisons of changes in functional

Table 4

Results of the DISTLM analysis used to identify environmental variables influencing the species and trait composition of the benthic macrofauna in a mangrove ecosystem in the Persian Gulf. P-values were obtained from 9999 permutations of residuals under a reduced model. SS (trace) = portion of sum of squares related to the analyzed environmental variable; Pseudo-F = F value by permutation; Bold values indicate significant level.

Environmental variables	Abundance			Trait modality		
	SS (trace)	Pseudo-F	P	SS (trace)	Pseudo-F	P
TOC	3426.2	1.088	0.380	234.11	0.367	0.888
TON	3362.9	1.067	0.401	529.79	0.839	0.519
Silt/Clay	5432.9	1.752	0.065	756.13	1.208	0.268
Temperature	10564.0	3.547	0.003	3944.80	7.172	0.0001
Salinity	5902.4	1.911	0.036	1095.30	1.772	0.117

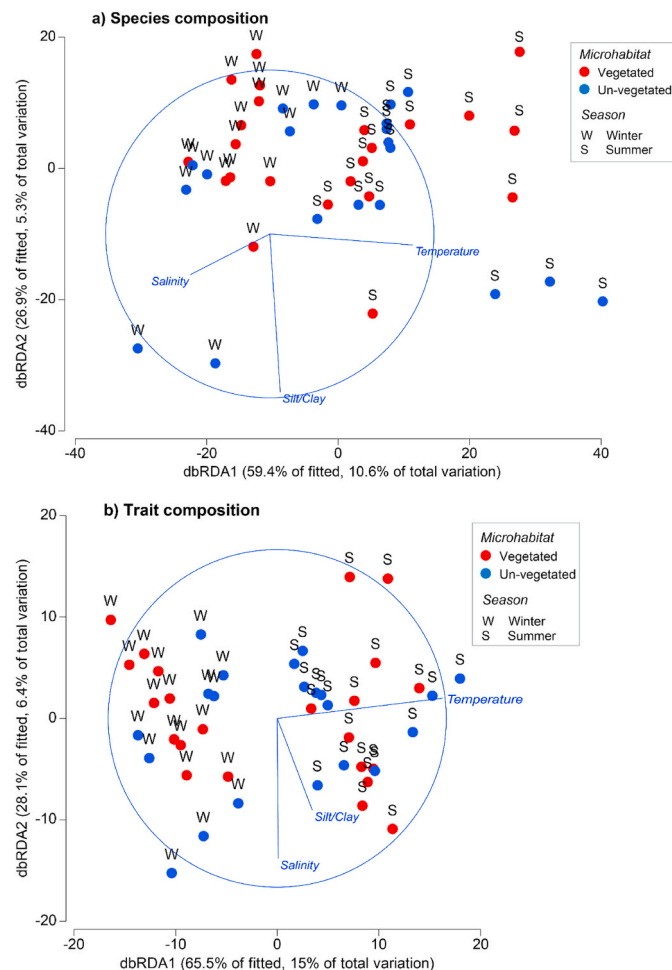


Fig. 6. Distance-based redundancy analysis (dbRDA), indicating the relationship between species (a) and trait (b) composition and environmental variables for the benthic macrofauna of a mangrove ecosystem in the Persian Gulf. The length and direction of vectors indicate the strength and direction of the relationship, respectively.

diversity, for example, along habitat gradients (Törnroos et al., 2013; van der Linden et al., 2017) or over large timescales covered by long-term monitoring (Clare et al., 2015; Meyer and Kröncke, 2019; Shojaei et al., 2021).

5. Conclusion

The results of the current study showed that the macrofaunal communities in an arid mangrove ecosystem were dominated by burrowers, surface deposit feeders, free-living, and large sized organisms with planktotrophic larval development. Low functional redundancy in the

mangrove macrofaunal community shows that small changes in species diversity in response to environmental fluctuations are likely to have profound effects on functional diversity. Therefore, the conservation of the ecological functions of the communities requires the conservation of a large proportion of the constituent species. The current study provides novel information regarding the functional structure of species-poor macrofaunal communities. Future research will show whether current management measures can adequately ensure the functioning of species-poor ecosystems.

Author statement

N.D. conceptualized the study, collected data, carried out statistical analysis and helped draft the manuscript; M.G.S. conceptualized and supervised the study, collected data, carried out statistical analysis, wrote the initial draft of the manuscript and critically revised the manuscript; R.N. participated in the design of the study, collected data and critically revised the manuscript. All authors approved the final manuscript for publication and agreed to be accountable for the result presented therein.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2021.107288>.

References

- Adame, M.F., Reef, R., Santini, N.S., Najera, E., Turschwell, M.P., Hayes, M.A., Masque, P., Lovelock, C.E., 2020. Mangroves in arid regions: ecology, threats, and opportunities. *Estuar. Coast Shelf Sci.* 106796. <https://doi.org/10.1016/j.ecss.2020.106796>.
- Agusto, L.E., Fratini, S., Jimenez, P.J., Quadros, A., Cannicci, S., 2020. Structural characteristics of crab burrows in Hong Kong mangrove forests and their role in

- ecosystem engineering. *Estuar. Coast Shelf Sci.* 106973. <https://doi.org/10.1016/j.ecss.2020.106973>.
- Alfaro, A.C., 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. *Estuar. Coast Shelf Sci.* 66, 97–110. <https://doi.org/10.1016/j.ecss.2005.07.024>.
- Allison, L.E., 1975. Organic carbon in: black CA. *Methods of soil analysis*. Am. Soc. Agron 2.
- Alongi, D.M., 2012. Carbon sequestration in mangrove forests. *Carbon Manag.* 3, 313–322. <https://doi.org/10.4155/cmt.12.20>.
- Amir, A.A., Duke, N.C., 2019. Distinct characteristics of canopy gaps in the subtropical mangroves of Moreton Bay, Australia. *Estuar. Coast Shelf Sci.* 222, 66–80. <https://doi.org/10.1016/j.ecss.2019.04.007>.
- Anderson, M.J., Gorley, R.N., Clarke, R.K., 2008. *PERMANOVA+ for Primer: Guide to Software and Statistical Methods*. PRIMER-E Ltd, Plymouth, UK, p. 214.
- Atwood, T.B., Connolly, R.M., Almahsheer, H., Carnell, P.E., Duarte, C.M., Lewis, C.J.E., Irigoien, X., Kelleway, J.J., Lavery, P.S., Macreadie, P.I., 2017. Global patterns in mangrove soil carbon stocks and losses. *Nat. Clim. Change* 7, 523–528. <https://doi.org/10.1038/nclimate3326>.
- Ball, M.C., 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. *Trees (Berl.)* 16, 126–139. <https://doi.org/10.1007/s00468-002-0169-3>.
- Beauchard, O., Verissimo, H., Queirós, A.M., Herman, P.M.J., 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecol. Indic.* 76, 81–96. <https://doi.org/10.1016/j.ecolind.2017.01.011>.
- Bellwood, D.R., Streit, R.P., Brandl, S.J., Tebbett, S.B., 2019. The meaning of the term function in ecology: a coral reef perspective. *Funct. Ecol.* 33, 948–961. <https://doi.org/10.1111/1365-2435.13265>.
- Beseres Pollack, J., Palmer, T., Montagna, P., 2011. Long-term trends in the response of benthic macrofauna to climate variability in the Lavaca-Colorado Estuary, Texas. *Mar. Ecol. Prog. Ser.* 436, 67–80. <https://doi.org/10.3354/meps09267>.
- Bolam, S.G., Eggleton, J.D., 2014. Macrofaunal production and biological traits: spatial relationships along the UK continental shelf. *J. Sea Res.* 88, 47–58. <https://doi.org/10.1016/j.seares.2014.01.001>.
- Boström, C., Törnroos, A., Bonsdorff, E., 2010. Invertebrate dispersal and habitat heterogeneity: expression of biological traits in a seagrass landscape. *J. Exp. Mar. Biol. Ecol.* 390, 106–117. <https://doi.org/10.1016/j.jembe.2010.05.008>.
- Bouillon, S., Koedam, N., Raman, A., Dehairs, F., 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia* 130, 441–448. <https://doi.org/10.1007/s004420100814>.
- Bouyoucos, G.J., 1962. Hydrometer method improved for making particle size analyses of soils 1. *Agron. J.* 54, 464–465. <https://doi.org/10.2134/agronj1962.00021962005400050028x>.
- Breine, N.T., De Backer, A., Van Colen, C., Moens, T., Hostens, K., Van Hoey, G., 2018. Structural and functional diversity of soft-bottom macrobenthic communities in the Southern North Sea. *Estuar. Coast Shelf Sci.* 214, 173–184. <https://doi.org/10.1016/j.ecss.2018.09.012>.
- Bremner, J., Rogers, S.I., Frid, C.L.J., 2006. Matching biological traits to environmental conditions in marine benthic ecosystems. *J. Mar. Syst.* 60, 302–316. <https://doi.org/10.1016/j.jmarsys.2006.02.004>.
- Bremner, J.M., Mulvaney, C.S., 1983. Nitrogen—total. *Methods soil Anal. Part 2 Chem. Microbiol. Prop.* 9, 595–624.
- Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.* 48, 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>.
- Chevone, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshw. Biol.* 31, 295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>.
- Chowdhury, R., Sutradhar, T., Begam, M.M., Mukherjee, C., Chatterjee, K., Basak, S.K., Ray, K., 2019. Effects of nutrient limitation, salinity increase, and associated stressors on mangrove forest cover, structure, and zonation across Indian Sundarbans. *Hydrobiologia* 842, 191–217. <https://doi.org/10.1007/s10750-019-04036-9>.
- Clare, D.S., Robinson, L.A., Frid, C.L.J., 2015. Community variability and ecological functioning: 40 years of change in the North Sea benthos. *Mar. Environ. Res.* 107, 24–34. <https://doi.org/10.1016/j.marenvres.2015.03.012>.
- Clarke, K.R., Gorley, R.N., 2006. *PRIMER Version 6: User Manual/tutorial*. PRIMER-E, Plymouth, p. 192.
- Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., 2018. Multiple facets of biodiversity drive the diversity–stability relationship. *Nat. Ecol. Evol.* 2, 1579–1587. <https://doi.org/10.1038/s41559-018-0647-7>.
- Degen, R., Aune, M., Bluhm, B.A., Cassidy, C., Kędra, M., Kraan, C., Vandepitte, L., Włodarska-Kowalczyk, M., Zhulay, I., Albano, P.G., Bremner, J., Grebmeier, J.M., Link, H., Morata, N., Nordström, M.C., Shojaei, M.G., Sutton, L., Zuschin, M., 2018. Trait-based approaches in rapidly changing ecosystems: a roadmap to the future polar oceans. *Ecol. Indic.* 91, 722–736. <https://doi.org/10.1016/j.ecolind.2018.04.050>.
- Dolédec, S., Chessel, D., Ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environ. Ecol. Stat.* 3, 143–166. <https://doi.org/10.1007/BF02427859>.
- Ellis, J., Nicholls, P., Craggs, R., Hofstra, D., Hewitt, J., 2004. Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. *Mar. Ecol. Prog. Ser.* 270, 71–82. <https://doi.org/10.3354/meps270071>.
- Floyd, M., Mizuyama, M., Obuchi, M., Sommer, B., Miller, M.G.R., Kawamura, I., Kise, H., Reimer, J.D., Beger, M., 2020. Functional diversity of reef molluscs along a tropical-to-temperate gradient. *Coral Reefs* 39, 1361–1376. <https://doi.org/10.1007/s00338-020-01970-2>.
- Franke, H.-D., Gutow, L., 2004. Long-term changes in the macrozoobenthos around the rocky island of Helgoland (German Bight, North Sea). *Helgol. Mar. Res.* 58, 303–310. <https://doi.org/10.1007/s10152-004-0193-3>.
- Freitas, R.F., Pagliosa, P.R., 2020. Mangrove benthic macrofauna: drivers of community structure and functional traits at multiple spatial scales. *Mar. Ecol. Prog. Ser.* 638, 25–38. <https://doi.org/10.3354/meps13260>.
- Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Griffin, J.N., 2014. Marine biodiversity and ecosystem functioning: what's known and what's next? *Oikos* 124, 252–265. <https://doi.org/10.1111/oik.01549>.
- Guillemot, N., Kulbicki, M., Chabanet, P., Vigliola, L., 2011. Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. *PLoS One* 6. <https://doi.org/10.1371/journal.pone.0026735> e26735–e26735.
- Gutow, L., Günther, C.-P., Ebbe, B., Schückel, S., Schuchardt, B., Dannheim, J., Darr, A., Pesch, R., 2020. Structure and distribution of a threatened muddy biotope in the south-eastern North Sea. *J. Environ. Manag.* 255, 109876. <https://doi.org/10.1016/j.jenvman.2019.109876>.
- Henseler, C., Nordström, M.C., Törnroos, A., Snickars, M., Pecuchet, L., Lindegren, M., Bonsdorff, E., 2019. Coastal habitats and their importance for the diversity of benthic communities: a species-and trait-based approach. *Estuar. Coast Shelf Sci.* 226, 106272. <https://doi.org/10.1016/j.jenvman.2019.109876>.
- Hewitt, J.E., Thrush, S.F., Dayton, P.D., 2008. Habitat variation, species diversity and ecological functioning in a marine system. *J. Exp. Mar. Biol. Ecol.* 366, 116–122. <https://doi.org/10.1016/j.jembe.2008.07.016>.
- Hickey, S.M., Callow, N.J., Phinn, S., Lovelock, C.E., Duarte, C.M., 2018. Spatial complexities in aboveground carbon stocks of a semi-arid mangrove community: a remote sensing height-biomass-carbon approach. *Estuar. Coast Shelf Sci.* 200, 194–201. <https://doi.org/10.1016/j.ecss.2017.11.004>.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naem, S., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35. <https://doi.org/10.1890/04-0922>.
- Janas, U., Burska, D., Kendzierska, H., Pryputniewicz-Flis, D., Łukawska-Matuszewska, K., 2019. Importance of benthic macrofauna and coastal biotopes for ecosystem functioning—Oxygen and nutrient fluxes in the coastal zone. *Estuar. Coast Shelf Sci.* 225, 106238. <https://doi.org/10.1016/j.ecss.2019.05.020>.
- Jennerjahn, T.C., 2020. Relevance and magnitude of Blue Carbon storage in mangrove sediments: carbon accumulation rates vs. stocks, sources vs. sinks. *Estuar. Coast Shelf Sci.* <https://doi.org/10.1016/j.ecss.2020.107027>, 107027.
- Jennerjahn, T.C., Gilman, E., Krauss, K.W., Lacerda, L.D., Nordhaus, I., Wolanski, E., 2017. Mangrove ecosystems under climate change. In: *Mangrove Ecosystems: A Global Biogeographic Perspective*. Springer, pp. 211–244. https://doi.org/10.1007/978-3-319-62206-4_7.
- Kristensen, D.K., Kristensen, E., Mangion, P., 2010. Food partitioning of leaf-eating mangrove crabs (Sesarinae): experimental and stable isotope (^{13}C and ^{15}N) evidence. *Estuar. Coast Shelf Sci.* 87, 583–590. <https://doi.org/10.1016/j.ecss.2010.02.016>.
- Leung, J.Y.S., 2015. Original research article: habitat heterogeneity affects ecological functions of macrobenthic communities in a mangrove: implication for the impact of restoration and afforestation. *Glob. Ecol. Conserv.* 4, 423–433. <https://doi.org/10.1016/j.gecco.2015.08.005>.
- Leung, J.Y.S., Cheung, N.K.M., 2017. Can mangrove plantation enhance the functional diversity of macrobenthic community in polluted mangroves? *Mar. Pollut. Bull.* 116, 454–461. <https://doi.org/10.1016/j.marpolbul.2017.01.043>.
- Mafi-Gholami, D., Mahmoudi, B., Zenner, E.K., 2017. An analysis of the relationship between drought events and mangrove changes along the northern coasts of the Persian Gulf and Oman Sea. *Estuar. Coast Shelf Sci.* 199, 141–151. <https://doi.org/10.1016/j.ecss.2017.10.008>.
- Mattone, C., Sheaves, M., 2017. Patterns, drivers and implications of dissolved oxygen dynamics in tropical mangrove forests. *Estuar. Coast Shelf Sci.* 197, 205–213. <https://doi.org/10.1016/j.ecss.2017.08.028>.
- McGovern, M., Poste, A., Oug, E., Renaud, P.E., Trannum, H.C., 2020. Riverine impacts on benthic biodiversity and functional traits: a comparison of two sub-Arctic fjords. *Estuar. Coast Shelf Sci.* 106774. <https://doi.org/10.1016/j.ecss.2020.106774>.
- McIntyre, S., Lavorel, S., Tremont, R.M., 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J. Ecol.* 31–44. <https://doi.org/10.2307/2261148>.
- McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* 9, 552–560. <https://doi.org/10.1890/110004>.
- Meyer, J., Kröncke, I., 2019. Shifts in trait-based and taxonomic macrofauna community structure along a 27-year time-series in the south-eastern North Sea. *PLoS One* 14, e0226410. <https://doi.org/10.1371/journal.pone.0226410>.
- Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. *Ecol. Lett.* 8, 391–400. <https://doi.org/10.1111/j.1461-0248.2005.00731.x>.
- Milesi, S.V., Dolédec, S., Melo, A.S., 2016. Substrate heterogeneity influences the trait composition of stream insect communities: an experimental in situ study. *Freshw. Sci.* 35, 1321–1329. <https://doi.org/10.1086/688706>.
- Murdiyarso, D., Purbopuspito, J., Kauffman, J.B., Warren, M.W., Sasmito, S.D., Donato, D.C., Manuri, S., Krisnawati, H., Taberima, S., Kurnianto, S., 2015. The potential of Indonesian mangrove forests for global climate change mitigation. *Nat. Clim. Change* 5, 1089–1092. <https://doi.org/10.1038/nclimate2734>.

- Naeem, S., Loreau, M., Inchausti, P., 2002. Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. *Biodivers. Ecosyst. Funct. Synth. Perspect.* 3–11.
- Nordhaus, I., Hadipudjana, F.A., Janssen, R., Pamungkas, J., 2009. Spatio-temporal variation of macrobenthic communities in the mangrove-fringed Segara Anakan lagoon, Indonesia, affected by anthropogenic activities. *Reg. Environ. Change* 9, 291–313. <https://doi.org/10.1007/s10113-009-0097-5>.
- Nordhaus, I., Salewski, T., Jennerjahn, T.C., 2017. Interspecific variations in mangrove leaf litter decomposition are related to labile nitrogenous compounds. *Estuar. Coast Shelf Sci.* 192, 137–148. <https://doi.org/10.1016/j.ecss.2017.04.029>.
- Nordhaus, I., Toben, M., Fauziyah, A., 2019. Impact of deforestation on mangrove tree diversity, biomass and community dynamics in the Segara Anakan lagoon, Java, Indonesia: a ten-year perspective. *Estuar. Coast Shelf Sci.* 227, 106300. <https://doi.org/10.1016/j.ecss.2019.106300>.
- Nordström, M.C., Aarnio, K., Törnroos, A., Bonsdorff, E., 2015. Nestedness of trophic links and biological traits in a marine food web. *Ecosphere* 6 (9), 1–14. <https://doi.org/10.1890/ES14-00515.1>.
- Norkko, A., Villnäs, A., Norkko, J., Valanko, S., Pilditch, C., 2013. Size matters: implications of the loss of large individuals for ecosystem function. *Sci. Rep.* 3, 2646. <https://doi.org/10.1038/srep02646>.
- R Development Core Team, R., 2011. R: A Language and Environment for Statistical Computing.
- Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. *Theor. Popul. Biol.* 21, 24–43.
- Reynolds, R.M., 2002. Oceanography. The Gulf Ecosystem: Health and Sustainability. Backhuys Publ, Leiden, Netherlands, pp. 53–61.
- Richards, D.R., Thompson, B.S., Wijedasa, L., 2020. Quantifying net loss of global mangrove carbon stocks from 20 years of land cover change. *Nat. Commun.* 11, 1–7. <https://doi.org/10.1038/s41467-020-18118-z>.
- Ruíf, A., Boix, D., Gascón, S., Sala, J., Batzer, D.P., 2013. Functional and phylogenetic relatedness in temporary wetland invertebrates: current macroecological patterns and implications for future climatic change scenarios. *PloS One* 8, e81739. <https://doi.org/10.1371/journal.pone.0081739>.
- Sahoo, G., Ansari, Z.A., Shaikh, J.B., Varik, S.U., Gauns, M., 2018. Epibiotic communities (microalgae and meiofauna) on the pneumatophores of *Avicennia officinalis* (L.). *Estuar. Coast Shelf Sci.* 207, 391–401. <https://doi.org/10.1016/j.ecss.2017.08.018>.
- Shahraki, M., Fry, B., Krumme, U., Rixen, T., 2014. Microphytobenthos sustain fish food webs in intertidal arid habitats: a comparison between mangrove-lined and un-vegetated creeks in the Persian Gulf. *Estuar. Coast Shelf Sci.* 149, 203–212. <https://doi.org/10.1016/j.ecss.2014.08.017>.
- Sheppard, C., Al-Husiani, M., Al-Jamali, F., Al-Yamani, F., Baldwin, R., Bishop, J., Benzioni, F., Dutrieux, E., Dulvy, N.K., Durvasula, S.R.V., 2010. The Gulf: a young sea in decline. *Mar. Pollut. Bull.* 60, 13–38. https://doi.org/10.1007/978-94-007-3008-3_17.
- Sheridan, P., 1997. Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, USA. *Estuar. Coast Shelf Sci.* 44, 455–469. <https://doi.org/10.1006/ecss.1996.0125>.
- Shojaei, M.G., Gutow, L., Dannheim, J., Pehlke, H., Brey, T., 2015. Functional diversity and traits assembly patterns of benthic macrofaunal communities in the southern North Sea. In: *Towards an Interdisciplinary Approach in Earth System Science*. Springer, pp. 183–195. https://doi.org/10.1007/978-3-319-13865-7_20.
- Shojaei, M.G., Gutow, L., Dannheim, J., Rachor, E., Schröder, A., Brey, T., 2016. Common trends in German Bight benthic macrofaunal communities: assessing temporal variability and the relative importance of environmental variables. *J. Sea Res.* 107 <https://doi.org/10.1016/j.seares.2015.11.002>.
- Shojaei, M.G., Gutow, L., Dannheim, J., Schröder, A., Brey, T., 2021. Long-term changes in ecological functioning of temperate shelf sea benthic communities. *Estuar. Coast Shelf Sci.* 249, 107097. <https://doi.org/10.1016/j.ecss.2020.107097>.
- Siqueira, A.C., Bellwood, D.R., Cowman, P.F., 2019. The evolution of traits and functions in herbivorous coral reef fishes through space and time. *Proc. R. Soc. B* 286, 20182672. <https://doi.org/10.1098/rspb.2018.2672>.
- Soper, F.M., MacKenzie, R.A., Sharma, S., Cole, T.G., Litton, C.M., Sparks, J.P., 2019. Non-native mangroves support carbon storage, sediment carbon burial, and accretion of coastal ecosystems. *Global Change Biol.* 25, 4315–4326. <https://doi.org/10.1111/gcb.14813>.
- Taupp, T., Wetzel, M.A., 2019. Functionally similar but taxonomically different: benthic communities in 1889 and 2006 in an industrialized estuary. *Estuar. Coast Shelf Sci.* 217, 292–300. <https://doi.org/10.1016/j.ecss.2018.11.012>.
- Teichert, N., Lepage, M., Sagouis, A., Borja, A., Chust, G., Ferreira, M.T., Pasquaud, S., Schinegger, R., Segurado, P., Argillier, C., 2017. Functional redundancy and sensitivity of fish assemblages in European rivers, lakes and estuarine ecosystems. *Sci. Rep.* 7, 1–11. <https://doi.org/10.1038/s41598-017-17975-x>.
- Torca, M., Campos, J.A., Herrera, M., 2019. Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. *Estuar. Coast Shelf Sci.* 218, 39–47. <https://doi.org/10.1016/j.ecss.2018.11.016>.
- Törnroos, A., Nordström, M.C., Bonsdorff, E., 2013. Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. *PloS One* 8. <https://doi.org/10.1371/journal.pone.0078910>.
- Usseglio-polatera, P., Bournaud, M., Richoux, P., Tachet, H., 2000. Biomonitoring through biological traits of benthic macroinvertebrates : how to use species trait databases ? https://doi.org/10.1007/978-94-011-4164-2_12, 153–162.
- van der Linden, P., Marchini, A., Smith, C.J., Dolbeth, M., Simone, L.R.L., Marques, J.C., Molozzi, J., Medeiros, C.R., Patrício, J., 2017. Functional changes in polychaete and mollusc communities in two tropical estuaries. *Estuar. Coast Shelf Sci.* 187, 62–73. <https://doi.org/10.1016/j.ecss.2016.12.019>.
- van der Linden, P., Patrício, J., Marchini, A., Cid, N., Neto, J.M., Marques, J.C., 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. *Ecol. Indic.* 20, 121–133. <https://doi.org/10.1016/j.ecolind.2012.02.004>.
- van der Wal, D., Lambert, G.I., Ysebaert, T., Plancke, Y.M.G., Herman, P.M.J., 2017. Hydrodynamic conditioning of diversity and functional traits in subtidal estuarine macrozoobenthic communities. *Estuar. Coast Shelf Sci.* 197, 80–92. <https://doi.org/10.1016/j.ecss.2017.08.012>.
- Wong, M.C., Dowd, M., 2015. Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in Atlantic Canada. *Estuar. Coast* 38, 2323–2336. <https://doi.org/10.1007/s12237-015-9967-x>.
- Wrede, A., Beermann, J., Dannheim, J., Gutow, L., Brey, T., 2018. Organism functional traits and ecosystem supporting services—A novel approach to predict bioirrigation. *Ecol. Indic.* 91, 737–743. <https://doi.org/10.1016/j.ecolind.2018.04.026>.
- zu Ermgassen, P.S.E., Mukherjee, N., Worthington, T.A., Acosta, A., da Rocha Araújo, A. R., Beil, C.M., Castellanos-Galindo, G.A., Cunha-Lignon, M., Dahdouh-Guebas, F., Diele, K., 2020. Fishers who rely on mangroves: modelling and mapping the global intensity of mangrove-associated fisheries. *Estuar. Coast Shelf Sci.* 106975. <https://doi.org/10.1016/j.ecss.2020.106975>.