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Ecological filtering and functional trait patterns in polychaete communities of the Arabian Gulf

Paravanparambil R. Jayachandran [a,*], Thadickal V. Joydas [a,**], Seerangan Manokaran [a], Jayanath Gopi [a], Sudhanshu Dixit [a], Mantodi Jima [b], Karuppasamy P. Manikandan [a], Mohamed Asharaf Thattathazhath [a], Premlal Panickan [a], Mohammed A. Qurban [c], Ali M. Qasem [d], Hamed Alghamdi [d], Diego Lozano-Cortés [d]

[a] Applied Research Center for Environment and Marine Studies, Research and Innovation, King Fahd University of Petroleum & Minerals, P. B. No. 1995, Dhahran, 31261, Saudi Arabia
[b] Department of Marine Biology, Microbiology and Biochemistry, School of Marine Sciences, Cochin University of Science and Technology, Cochin, 682016, Kerala, India
[c] National Center for Wildlife, Riyadh 12746, Saudi Arabia
[d] Environmental Protection Department, Saudi Aramco, Dhahran, 31311, Saudi Arabia

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ABSTRACT

Functional traits provide a mechanistic link between species attributes and ecosystem processes, offering insights into community responses to environmental gradients. This study examined how habitat heterogeneity structures macrobenthic polychaete functional diversity along the Saudi Arabian Gulf coast (Khafji to Ras Abu Qamis). Benthic habitats were classified into shallow, intermediate, and deep zones. Functional diversity indices—functional dispersion (FDis), functional richness (FRic), and Rao's quadratic entropy (RaoQ) were applied alongside RLQ and fourth-corner analyses to assess trait–environment relationships. Shallow and intermediate zones exhibited significantly higher functional diversity ($p < 0.01$), with traits such as small body size, infaunal position, burrowing mobility, and carnivory dominating. Deeper habitats showed reduced FRic and greater trait convergence, associated with fine sediments. Functional redundancy (FRed), over-redundancy (FORed), and vulnerability (FVuln) assessments revealed that most functional entities were supported by a single species, indicating low ecological buffering capacity. Variance Partitioning Analysis attributed significant portion of functional diversity variation to sediment properties, with grain size (Φ) identified as the primary driver. Structural Equation Modeling confirmed grain size as a significant negative predictor of FDis, FRic, and RaoQ. These findings underscore the role of sediment structure and depth-related environmental gradients in shaping the functional composition of polychaetes. The low redundancy observed highlights the vulnerability of Gulf benthic systems to biodiversity loss, reinforcing the need for sediment-focused conservation strategies.

1. Introduction

Benthic habitats of the Arabian Gulf, including mangroves, seagrass beds, coral reefs, mudflats, and sandy substrates, support biodiversity and provide ecosystem services such as carbon storage and coastal protection (Naser, 2011). However, climate change and human activity are causing significant degradation and loss of these habitats (Wabnitz et al., 2018). This poses a threat to macrobenthic communities, which play crucial roles in ecosystem functioning (Joydas et al., 2015a; Wei et al., 2016). Polychaetes, a dominant component of macrobenthos in the Saudi Arabian Gulf, play essential roles in organic matter decomposition, sediment bioturbation, and benthic–pelagic coupling (Joydas et al., 2011, 2012, 2015b; Kristensen and Kostka, 2005; Lozano-Cortés et al., 2019; Martins and Barros, 2022). These communities exhibit spatial heterogeneity influenced by factors such as bathymetry, oxygen levels, and substrate type (Braeckman et al., 2010). Functional trait analysis, including environmental position and feeding modes, helps understand the ecological roles of the species and their responses to environmental gradients (Dong et al., 2021; Gimenez and Lana, 2020; Jayachandran et al., 2019, 2022). Although habitat structure has been

* Corresponding author.
** Corresponding author.
E-mail addresses: j.rajakumar@kfupm.edu.sa (P.R. Jayachandran), tvjoydas@kfupm.edu.sa (T.V. Joydas).

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well studied, spatial variation in functional trait composition and diversity among benthic ecosystems remains underexplored. Understanding these aspects is crucial for managing ecosystems under natural and anthropogenic pressures.

Functional traits are physical, behavioral, or life history characteristics that shape how species interact with their environment offering a process-based way to understand biodiversity through the roles organisms play in ecosystems, not just by their presence or abundance (Hu et al., 2022). The distribution of functional traits in benthic polychaete communities is influenced by various environmental factors (Hu et al., 2019; Jumars et al., 2015). Therefore, a better understanding of the relationship between functional traits and corresponding environmental conditions is crucial for understanding the mechanisms driving their distributions and functional responses. Dolédec et al. (1996) and Legendre et al. (1997) developed two different methods to analyze data sets on environmental variables (R), species abundance (L), and functional traits (Q) simultaneously. These methods are known as RLQ analysis and the fourth-corner approach. The combination of these methodologies has been employed in numerous investigations to explore the correlations between macrobenthic functional characteristics and distinct environmental parameters (Hu et al., 2022). Functional diversity (FD) is a core dimension of biodiversity, influencing ecosystem dynamics, resilience, energy transfer, and biogeochemical cycling. It is widely used to evaluate how habitat heterogeneity affects the ecological roles of benthic communities (Laliberté and Legendre, 2010).

The Arabian Gulf's benthic ecosystem comprises diverse microhabitats, including seagrass beds, coral reefs, and sandy and muddy substrates shaped by natural and human-induced pressures (Joydas et al., 2024). However, functional traits and diversity of macrobenthic polychaetes remain poorly understood in this region, despite their ecological

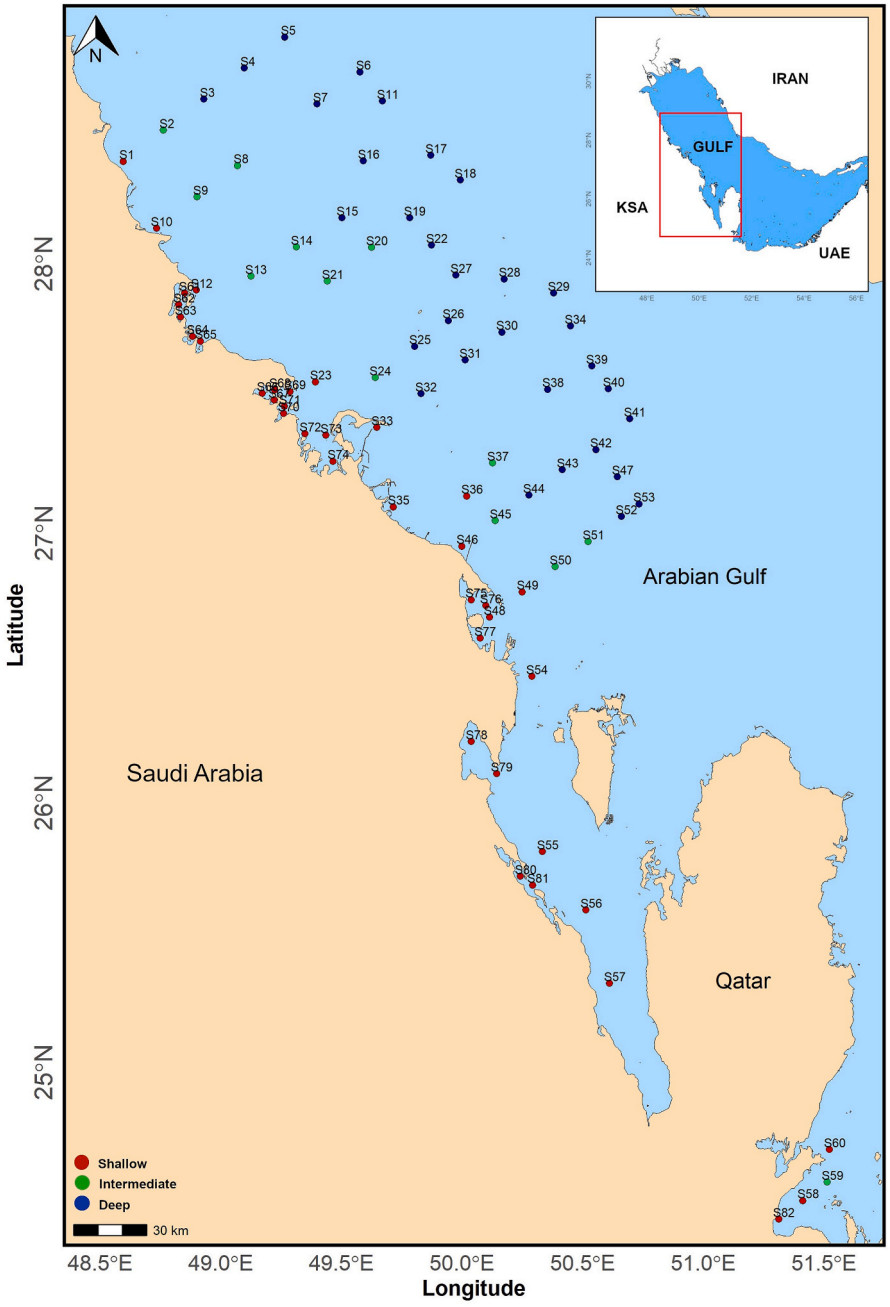

Fig. 1. Map showing the sampling locations, indicated by points (red for shallow, green for intermediate, and navy blue for deeper stations). The Inset map shows the study area within the Arabian Peninsula. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

significance. We hypothesise that sediment properties, particularly grain size, exert a stronger influence than water quality variables on the functional trait composition and diversity of macrobenthic polychaete communities along the Saudi Arabian coast of the Arabian Gulf. To test this, we applied RLQ and fourth corner analyses to examine trait–environment relationships, calculated multiple functional diversity indices (FRic, FDis, RaoQ), and assessed ecosystem resilience using measures of functional redundancy (FRed), over redundancy (FORed), and functional vulnerability (FVuln). These integrated approaches provide a comprehensive understanding of the relative importance of environmental drivers in structuring benthic functional diversity, with implications for biodiversity conservation and sediment-based management strategies in the region.

2. Materials and methods

2.1. Study area

The investigation was conducted within the territorial waters of Saudi Arabia in the Arabian Gulf, extending from Khafji to Ras Abu Qamis (Fig. 1, Supplementary Table S1). Sampling was conducted at 82 designated stations using King Fahd University of Petroleum and Minerals (KFUPM) research vessels between August and October 2013. These designated stations encompassed depth ranges from 2 to 59 m (Fig. 1). The stations were categorized by depth into three distinct zones: shallow (2–14 m), intermediate (15–29 m), and deeper (30–59 m). For safety reasons, no samples were collected near offshore oil infrastructure or platforms.

2.2. Sampling methodology

Two sets of sediment samples were collected from each site using a standard van Veen grab sampler with a bite area of 0.1 m^2. These samples were processed separately by sieving through a 500 μm mesh, fixed in 4 % buffered formalin, and stored individually. Subsamples (~500 g per station) obtained from a third grab sample were used for the analysis of sediment and other variables. Subsamples were transported in ice-packed coolers and stored at 4 °C until analysis. On-site measurements of temperature, salinity, and dissolved oxygen (DO) were conducted using a multiprobe water quality instrument (YSI EXO2 Multiparameter Sonde).

2.3. Sample analysis

Preserved macrobenthic organisms were stained with Rose Bengal overnight. Polychaetes were extracted and identified to the lowest possible taxonomic level using stereomicroscopy and light microscopy. Species identification was conducted using standard taxonomic references (Australian Museum, 2022; Day, 1967; Fauchald, 1977; Fauchald and Jumars, 1979; Glasby and Fauchald, 2003). Species names were verified via the World Register of Marine Species (WoRMS). Density (N) was expressed in individuals per square meter (ind. m^{-2}). Species diversity was assessed across depth zones using species richness (S), Shannon diversity index (H' ($\log_{10}$)), and Pielou's evenness (J'), based on abundance data processed in PRIMER *v7* (Clarke and Gorley, 2015).

2.4. Environmental parameters

Grain size was analyzed using a combined sieving–pipette method (Carver, 1971), with mean grain size calculated using the Folk and Ward (1957) method. Total organic carbon (TOC) in sediments was measured in a TOC analyzer (Shimadzu TOC ASI-V). Sediment samples for inorganic and organic contaminant analysis were freeze-dried, ground, and homogenized to ensure consistency. Metals and metalloids, including arsenic (As), barium (Ba), chromium (Cr), copper (Cu), mercury (Hg), nickel (Ni), lead (Pb), and vanadium (V), were extracted by following the standard guidelines of US EPA Method 3050 B (1996) with concentrations measured according to US EPA Method 6010C (2007) in a PerkinElmer DV 8000 inductively coupled plasma optical emission spectrometer (ICP-OES). Mercury was analyzed using the direct combustion atomic absorption method (US EPA Method 7473, 2007) in the Nippon MA 3000 mercury analyzer. Polycyclic Aromatic Hydrocarbons (PAHs) were extracted using US EPA Method 3550C (2007), and aromatic fractions were analyzed by GC-MS in selected ion monitoring (SIM) mode (US EPA Method 8270 D, 2007).

2.5. Functional trait analysis

Information on polychaete functional traits (Table 1) was obtained from the literature (Fauchald and Jumars, 1979; Jumars et al., 2015; Macdonald et al., 2010) and databases such as SeaLifeBase (2025), BIOTIC: Biology Traits Information (2025), WoRMS: World Register of Marine Species (2025), and Polytraits (2025). Traits were inferred based on related species when specific trait data were unavailable. A fuzzy coding system was used to assign trait affinities from 0 (no affinity) to 3 (strong affinity), following Hu et al. (2022).

2.6. RLQ and fourth-corner analyses

RLQ and fourth-corner analyses were employed to assess how functional traits of macrobenthic polychaetes varied across depth zones. In the RLQ analysis, data on environmental variables (R), species abundance (L), and functional traits (Q) were analyzed using Hill-Smith analysis, correspondence analysis (CA), and principal component analysis (PCA), respectively (Dray, 2013; Dray et al., 2014). Global significance was tested using a Monte Carlo procedure (49,999 permutations) under models 2 and 4. Model 2 tests environmental effects on species distributions given fixed traits, while Model 4 tests trait effects under fixed environmental conditions (Dray et al., 2014). Since RLQ analysis alone does not identify specific environmental variables affecting individual traits, fourth-corner analysis was applied to determine the significance of trait-environment associations (Dray et al., 2014). Both RLQ

Table 1
Functional trait classification of macrobenthic polychaete species in the Arabian Gulf (modified from Hu et al., 2022).

Functional trait	Trait modality	Abbreviation
Body size	Very small (<1 cm)	B1
	Small (1–3 cm)	B2
	Medium (3–10 cm)	B3
	Large (>10 cm)	B4
Environmental position	Infauna	P1
	Epifauna	P2
Mobility	Sessile	M1
	Tube-builder	M2
	Burrower	M3
	Swimmer	M4
	Crawler	M5
Feeding mode	Carnivore	F1
	Surface deposit-feeder	F2
	Sub-surface deposit-feeder	F3
	Suspension-feeder	F4
	Herbivorous	F5
AMBI ecological group	Sensitive Species	AI
	Indifferent Species	AII
	Tolerant Species	AIII
	Second-order Opportunistic Species	AIV
	First-order Opportunistic Species	AV
Lifespan	Short (<1 year)	L1
	Medium (1–5 years)	L2
	Long (>5 years)	L3
Substrate affinity	Sand	S1
	Gravel	S2
	Mud sand	S3
	Mud	S4
	Seagrass	S5

and fourth-corner analyses were conducted using the 'ade4' package in R (Dray and Dufour, 2007).

2.7. Functional diversity analysis

Three functional diversity indices—functional dispersion (FDis), functional richness (FRic), and Rao's Quadratic Entropy (RaoQ)—were computed using the FD package in R (Laliberté and Legendre, 2010). These indices encompass functional richness (FRic) and functional dispersion (FDis), which quantify the extent of trait space utilized by a community, the arrangement of traits within this space, and the variability and spatial distribution of species trait assemblages. Rao's quadratic entropy (RaoQ) differs from FRic and FDis by explicitly incorporating both species abundances and pairwise functional dissimilarities, offering a more integrative view of functional diversity. Variance Partitioning Analysis (VPA), performed using the vegan package (Oksanen et al., 2019), quantified the relative contributions of sediment properties and water quality to variations in functional diversity. Analyzing the uniqueness and recurrence of species traits offered insights into ecosystem resilience through measures of redundancy and vulnerability. Functional redundancy (FRed), functional over-redundancy (FORed), and functional vulnerability (FVuln) were quantified for each functional entity (FE) to assess trait resilience and potential ecosystem risk (Villéger et al., 2008, 2011), conducted in R using the mFD package (Magneville et al., 2022). These metrics help estimate the impact of species loss on ecosystem functioning and highlight critical functional roles for conservation (Coker et al., 2025; Denis et al., 2019). FRed reflects how many species share the same trait combination, indicating resilience to species loss. FORed identifies cases where some traits are overrepresented, potentially masking underlying vulnerabilities. FVuln highlights traits supported by only one or a few species, flagging critical points of ecosystem fragility (Fetzer et al., 2015; Pombo-Ayora et al., 2020, 2024).

2.8. Structural Equation Modeling

Structural Equation Modeling (SEM) has emerged as a powerful statistical technique for analyzing complex relationships among variables (Shi et al., 2022). SEM was performed using the lavaan package to test both direct and indirect relationships between functional diversity indices and environmental variables (Rosseel, 2012). This approach identifies both direct and indirect environmental influences on functional diversity, enhancing our understanding of key ecological processes (Lefcheck, 2016; Rosseel, 2012). The readxl package (Wickham et al., 2019) was used to import data from Excel files, and the semPlot package (Epskamp et al., 2017) was employed to generate path diagrams visualizing the SEM results. Statistical analyses were conducted in R (R Core Team, 2023).

3. Results

3.1. Environmental parameters

The environmental parameters measured during this study, encompassing both sediment and water characteristics, are presented in Table 2. Significant differences ($p < 0.001$) were observed among depth zones in terms of temperature, salinity, dissolved oxygen, and sediment composition (sand, silt, and clay). Pairwise comparisons revealed the most pronounced differences between shallow and deep zones across all measured parameters (Table 2). However, no significant variation was found for TOC ($p = 0.149$), arsenic (As; $p = 0.239$), and mercury (Hg; $p = 0.279$) between different depth zones.

3.2. Functional trait composition

A total of 29 functional trait modalities were assigned to 228 polychaete species (Fig. 2), revealing distinct distribution patterns across depth zones (Fig. S1). Trait composition varied with depth, though small-sized (B2), infaunal (P1), and burrowing (M3) taxa remained consistently dominant across zones. Sessile forms (M1) were not common in soft bottom habitats. In shallow zones, small-sized (B2: 45.72 %) and short-lived species (L2: 71.73 %) were prevalent. Infaunal organisms (P1: 58.68 %) were primarily barrowing (M3: 44.42 %), with carnivores (F1: 38.65 %) and surface deposit-feeders (F2: 31.92 %) comprising the main feeding groups. Ecologically indifferent species (AII: 43.28 %) dominated, with a preference for muddy sand (S3: 36.69 %). Seagrass-associated taxa also showed increased representation in this zone. Intermediate zones exhibited a similar profile, characterized by high proportions of small-sized (B2: 45.75 %), infaunal (P1: 60.82 %), burrowing taxa (M3: 48.75 %), and a balanced mix of carnivores (F1: 37.08 %) and surface deposit-feeders (F2: 30.71 %). Tolerant species (AII: 35.04 %) and medium-lifespan taxa (L2: 76.83 %) were common, with muddy sand (S3: 36.63 %) remaining the dominant substrate. In deeper zones, small (B2: 42.31 %) and medium-sized (B3: 35.84 %) organisms dominated, alongside infaunal (P1: 66.73 %) and burrowing (M3: 48.64 %) forms. Tube-building forms were relatively more abundant in deeper soft-sediment habitats, comprising 20.37 % of the assemblage (M2). Surface deposit-feeders (F2: 35.00 %) slightly exceeded carnivores (F1: 33.61 %) in prevalence. Indifferent (AII: 36.99 %) and medium-lifespan (L2: 75.41 %) species remained common, with a clear shift toward muddy sand (S3: 38.78 %) and mud (S4: 22.55 %) substrates. First-order opportunistic taxa were more abundant in deeper zones, while very small-sized species were less frequent. Across all zones, indifferent ecological groups and medium-lifespan taxa were consistently dominant, particularly in association with muddy sand substrates (Supplementary Table S2).

Table 2
Environmental variables associated with Arabian Gulf depth zones.

Environmental variable	Depth zones (mean ± SD)		
	Shallow	Intermediate	Deeper
Sediment properties			
Sand (%)	80.4 ± 27.7^{A}	72.7 ± 25.4^{A}	53.3 ± 25.8^{B}
Silt (%)	12.8 ± 18.4^{A}	19.8 ± 23.5^{A}	32.3 ± 23.8^{B}
Clay (%)	6.8 ± 12.4^{A}	7.5 ± 6.9^{A}	14.4 ± 11^{B}
Silt/clay (%)	19.6 ± 27.7^{A}	27.3 ± 25.4^{A}	46.7 ± 25.8^{B}
Grain size (phi; Φ)	2.4 ± 1.9^{A}	2.9 ± 1.6^{A}	4.2 ± 1.4^{B}
Total organic carbon (%)	0.5 ± 0.2^{A}	0.4 ± 0.1^{A}	0.4 ± 0.1^{A}
PAHs (μg kg^{-1})	14.5 ± 22.9^{A}	1.4 ± 3^{B}	2.1 ± 5.8^{B}
As (mg kg^{-1})	3.7 ± 2.3^{A}	11.1 ± 15.7^{A}	3.1 ± 2.6^{A}
Ba (mg kg^{-1})	22.4 ± 11.6^{A}	34.1 ± 38^{A}	155.8 ± 224.4^{B}
Cr (mg kg^{-1})	12.8 ± 12.3^{A}	11.4 ± 11.9^{A}	37.6 ± 13.5^{B}
Cu (mg kg^{-1})	4 ± 4.8^{A}	2.9 ± 3.3^{A}	8.4 ± 3.3^{B}
Hg (mg kg^{-1})	0.03 ± 0.01^{A}	0.04 ± 0.02^{A}	0.03 ± 0.02^{A}
Ni (mg kg^{-1})	14 ± 16.2^{A}	12.5 ± 14.4^{A}	43.6 ± 17.5^{B}
Pb (mg kg^{-1})	2.5 ± 2.8^{A}	3.9 ± 3.9^{A}	3.7 ± 1.3^{B}
V (mg kg^{-1})	12.3 ± 11.3^{A}	8.3 ± 7.3^{A}	23.4 ± 7^{B}
Water quality			
Actual depth (m)	5.3 ± 3.5^{A}	22.3 ± 4.3^{B}	46.5 ± 8.3^{C}
Temperature (∘C)	33 ± 1.8^{A}	31.1 ± 2.3^{B}	28.7 ± 1.6^{C}
Salinity	47.8 ± 6.2^{A}	42 ± 3.2^{B}	39.8 ± 0.3^{C}
Dissolved oxygen (mg l^{-1})	5.4 ± 0.4^{A}	5.5 ± 0.5^{A}	5.9 ± 0.2^{B}

Values in each column sharing the same letters (A, B, C) are not significantly different (Bonferroni test, $p > 0.05$).

3.3. RLQ and fourth-corner analyses

The global RLQ test revealed a significant relationship between functional trait composition and environmental variables (model 2: $p = 0.00002$; model 4: $p = 0.00004$). RLQ ordination explained a total inertia of 0.7018, with the first two RLQ axes accounting for 95.77 % of the total inertia. The first RLQ axis explained 85.51 % of the total

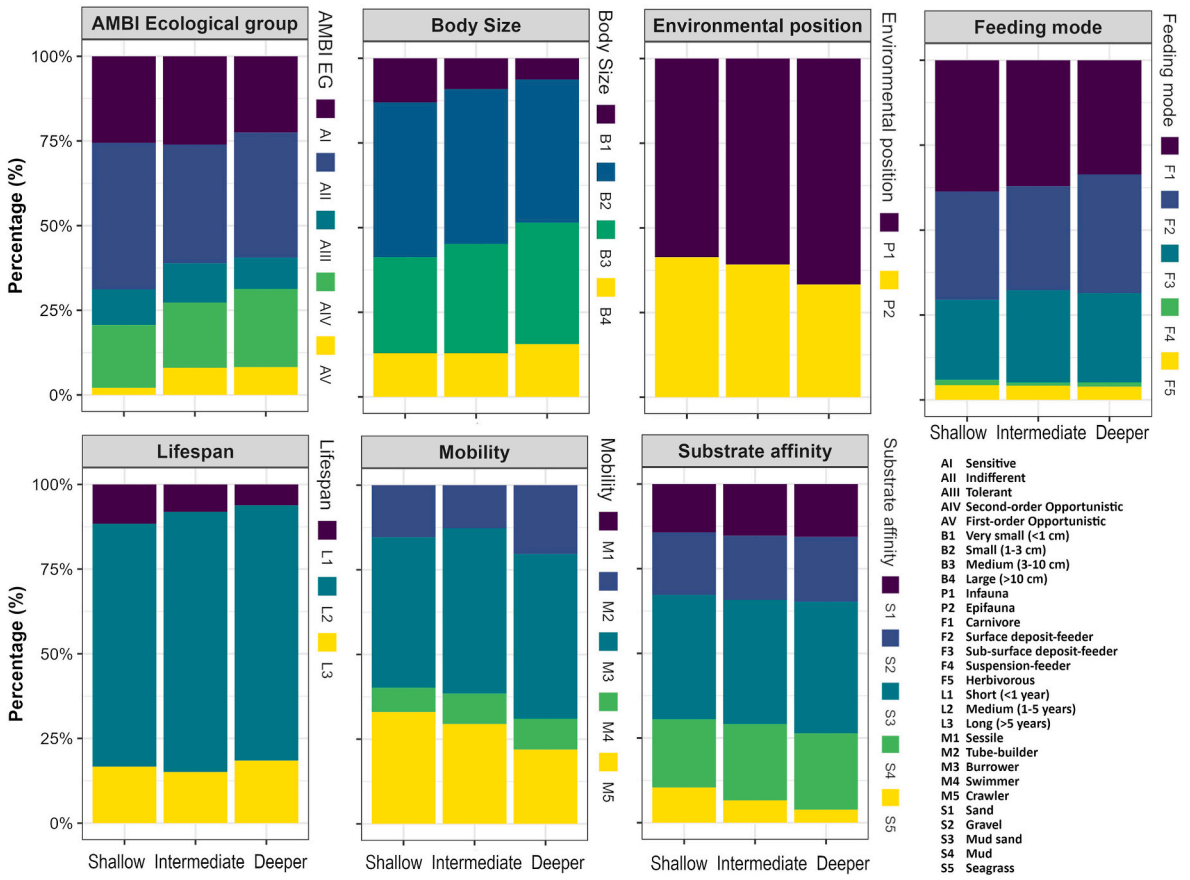

Fig. 2. The distribution of macrobenthic polychaete functional traits across three depth zones.

variance, while the second axis contributed 10.25 %. RLQ and fourth-corner analyses revealed several significant relationships between environmental variables and functional traits. The body size modality, very small (B1) showed strong negative correlations with depth, silt, clay, and metals, and a positive correlation with sand and TOC. Medium (B3) exhibited a positive relationship with silt, clay, and metals, and a negative relationship with sand. Large (B4) showed a positive relationship with TOC. Epifauna (P2) had a negative relationship with clay. Crawlers (M5) were negatively correlated with silt, clay, and metals in sediment, but positively correlated with sandy substrates. In terms of feeding group modality, surface deposit-feeders (F2) showed a positive relationship with TOC, suggesting that organic-rich sediments favor surface deposit-feeders. At the same time, suspension feeders (F4) had a positive relationship with sandy substrates and higher salinity, and a negative relationship with clay/silt substrates. The ecological group of first order opportunistic species (AV) was positively correlated with clay sediment. For the life span modality, short-lived species (L1) showed a positive relationship with TOC content in sediment. The substrate affinity trait of seagrass associated species (S5) showed a negative relationship with silt, clay, and metals, but a positive relationship with sand. Sand, depth, silt, clay, and metals were significantly associated with the first RLQ axis, while Hg and PAHs were linked to the second axis (Supplementary Fig. S1 and S2). While TOC, salinity and temperature were correlated with both axes (Fig. 3).

3.4. Species diversity

Shallow zones exhibited the highest average macrobenthic diversity, with a Shannon diversity index (H' ($\log_{10}$)) of 5.158, Pielou's evenness (J') of 0.99, and species richness (S) of 44.6, reflecting well-structured and diverse communities. Intermediate zones showed moderately lower diversity, with H' ($\log_{10}$) = 4.87, J' = 0.99, and S = 34.13, while deeper zones had the lowest average species richness and marginally reduced diversity overall (H' ($\log_{10}$) = 5.07, J' = 0.99, S = 37.25). Despite depth-related differences, high evenness across zones suggests a relatively balanced distribution of species throughout. These patterns highlight a subtle depth-related gradient, where diversity and richness tend to decrease with increasing depth.

3.5. Functional diversity

The functional diversity of the benthic polychaete communities varied with the different depth zones, especially between shallow and deeper zones for FDis ($p < 0.01$) and RaoQ ($p < 0.01$) (Fig. 4). No significant differences were found between intermediate and either shallow or deeper zones. Spearman correlation analysis of functional diversity metrics across depth zones is shown in Fig. 5. In all depth zones, FDis was significantly positively correlated with RaoQ ($p < 0.001$). A significant positive correlation was observed between RaoQ and FRic in both shallow ($p < 0.001$) and deep zones ($p < 0.01$). Additionally, FDis and FRic showed a positive correlation in shallow ($p < 0.001$) and deeper zones ($p < 0.05$). The Variance Partitioning Analysis (VPA) results indicated that sediment properties played a more influential role in shaping functional diversity of benthic polychaete communities; sediment quality variables explain 27.11 %, while water quality variables explain 14.92 % (Supplementary Fig. S3).

The functional diversity analysis across the surveyed area identified 227 polychaete species, which were categorized into 138 functional entities (FEs), yielding an average of 1.64 species per functional entity (FE). A significant portion (69 %) of these FEs were functionally vulnerable, represented by a single species, while the remaining 31 % exhibited over-redundancy, comprising two or more species (Fig. 6).

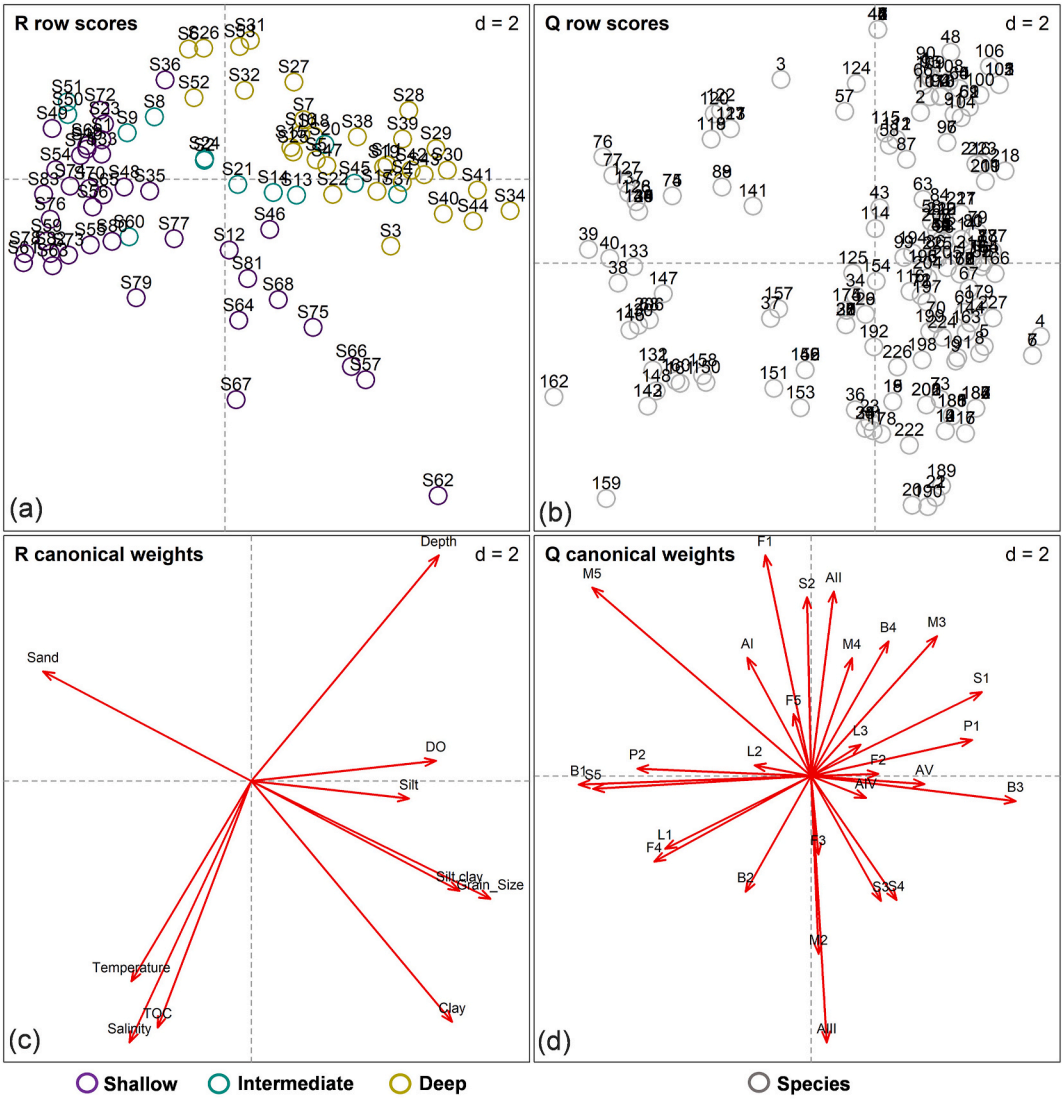

Fig. 3. Results of the first two axes of the RLQ analysis: covariation of (a) sampling sites (b) species (refer to the serial number corresponding to each species in Supplementary Table 2), (c) environmental variables, and (d) trait modalities (see Table 1 for full forms of abbreviations). Sampling site details are in Supplementary Table S1.

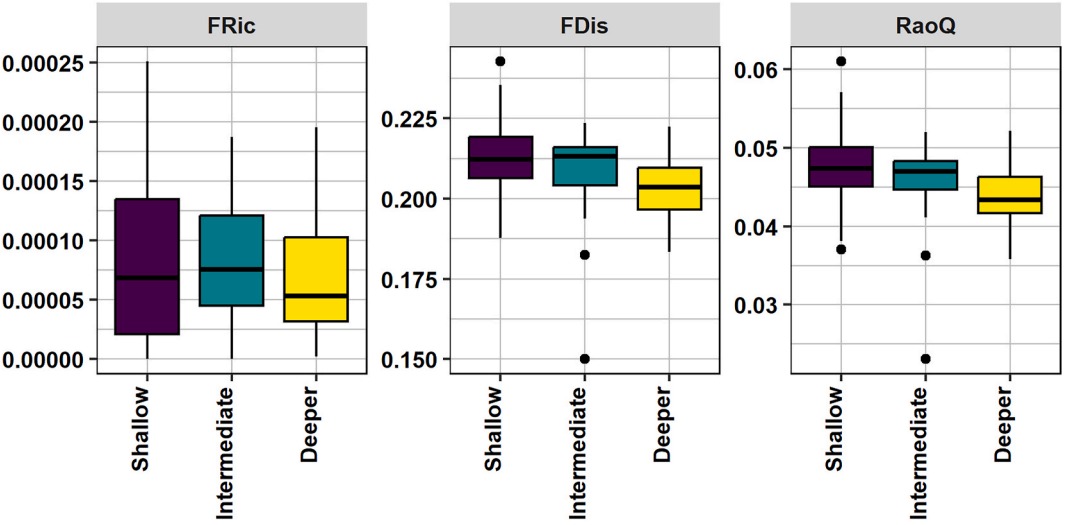

Fig. 4. Functional diversity of macrobenthic polychaete communities in the three depth zones.

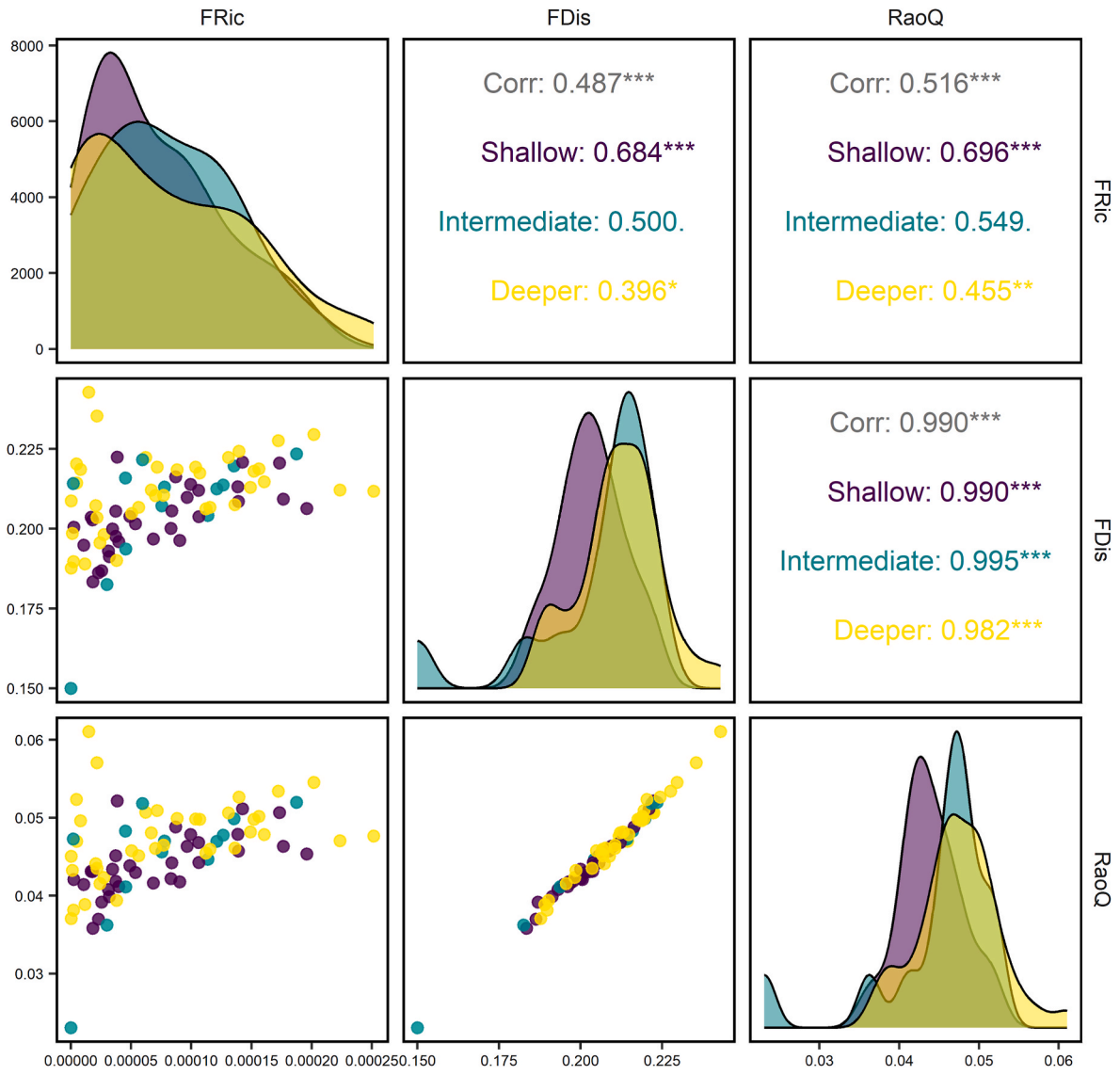

Fig. 5. Spearman's rank correlation analysis of functional diversity metrics across three depth zones. *$p < 0.05$, ***$p < 0.001$.

Across different depth zones, species richness ranged from 131 to 180, with functional entities varying between 94 and 121. Functional redundancy (FRed) ranged from 1.39 to 1.49, functional over-redundancy (FORed) varied between 20 % and 25 %, and functional vulnerability (FVuln) spanned 75 %–80 %. The most over-redundant FEs included up to six or seven species, a pattern consistent across depth zones.

The Structural Equation Modeling (SEM) framework allows for evaluating the direct and indirect effects of multiple predictors (Fig. 7). Fit indices met the conventional criteria for a perfect fit (CFI and TLI $\geq$0.95; RMSEA and SRMR $\leq$0.05), with all values indicating excellent model performance (CFI/TLI = 1.000; RMSEA/SRMR = 0.000). The specified model included depth, temperature, salinity, DO, grain size (Φ) and silt + clay percentage as predictors for FRic, FDis, and RaoQ (Fig. 7). Grain size (Φ) emerged as a significant negative predictor for all three functional diversity indices, such as FDis ($\beta = -0.758$, $p = 0.005$), RaoQ ($\beta = -0.724$, $p = 0.008$), and marginally for FRic ($\beta = -0.617$, $p = 0.050$). Other environmental variables (e.g., depth, temperature, salinity, TOC, silt + clay) were positively correlated with diversity indices but lacked statistical significance. Depth had negligible influence on the indices: depth to FRic: −0.022 ($p = 0.910$), depth to FDis: −0.014 ($p = 0.933$), depth to RaoQ: −0.002 ($p = 0.989$). Significant covariances were observed among FRic, FDis, and RaoQ, indicating interrelationships among these indices: FRic and FDis: 0.234 ($p = 0.005$), FRic and RaoQ: 0.235 ($p = 0.005$), FDis and RaoQ: 0.619 ($p = 0.000$). Residual variance suggests the influence of unmeasured environmental or biological factors influencing functional diversity.

4. Discussion

This study demonstrates that macrobenthic polychaete communities in the Arabian Gulf exhibit pronounced depth-wise zonation, primarily structured by sediment heterogeneity and associated environmental gradients (Jayachandran et al., 2024). Sediment composition shifted markedly with depth, transitioning from coarse sands in the shallow subtidal to finer silts and clays in deeper habitats (Joydas et al., 2015a, 2024; Lozano-Cortés et al., 2019). This granulometric gradient, combined with changes in salinity, oxygen availability, and organic enrichment, acts as a strong ecological filter influencing both taxonomic and functional trait composition (Brown and Thatje, 2014; Martins and Barros, 2022; Meijer et al., 2023; Miri et al., 2023; Sahu and Thiruchitrambalam, 2025).

Shallow, dynamic habitats with high productivity and detrital accumulation support a diverse array of small-bodied, surface-feeding,

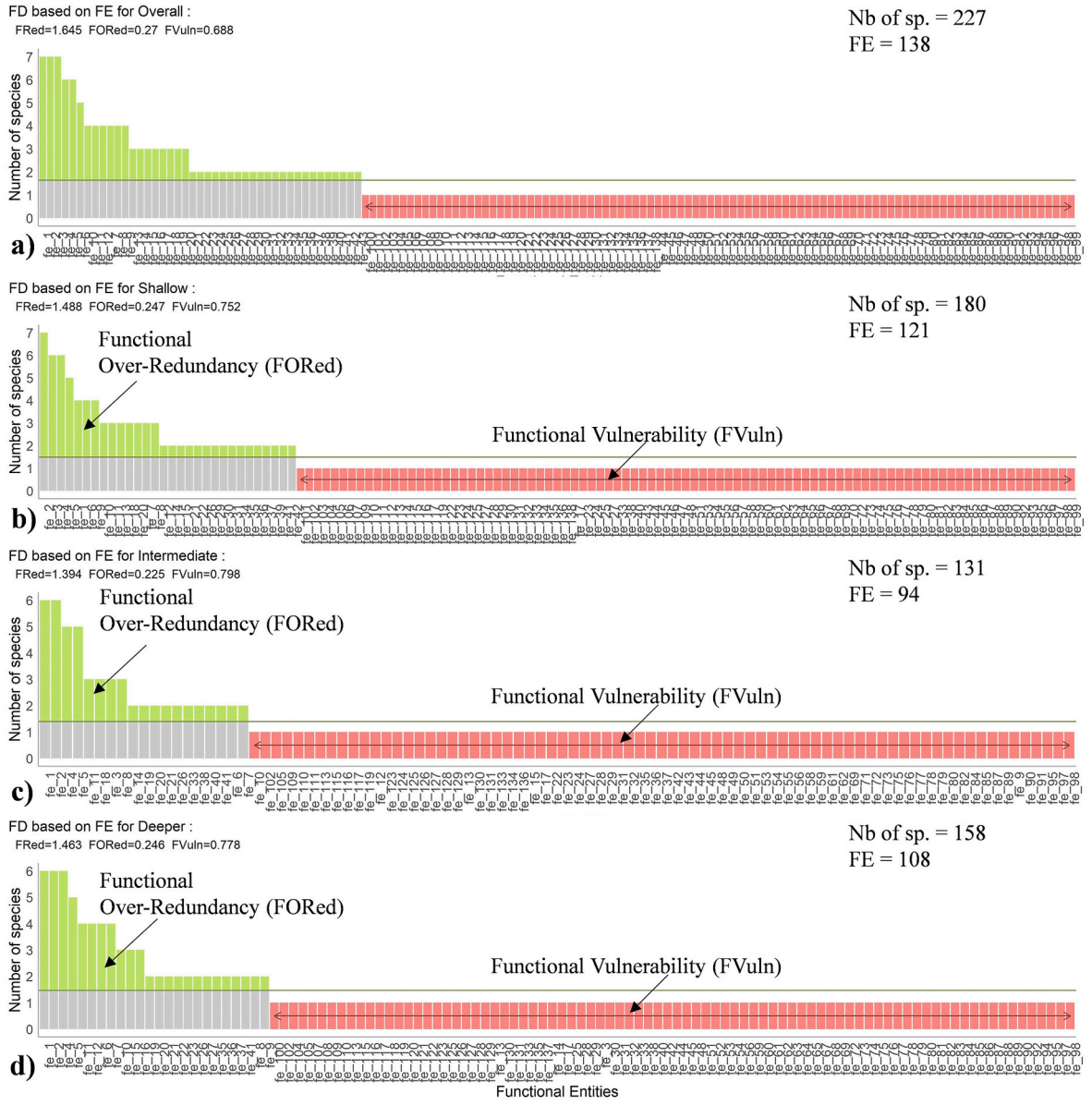

Fig. 6. Functional over-redundancy, functional redundancy, and functional vulnerability based on functional entities across (a) overall stations, (b) shallow zone, (c) intermediate zone, and (d) deeper zone. (FD: functional diversity, FE: functional entity).

mobile taxa traits associated with opportunistic strategies and rapid colonization. Species such as *Prionospio* sp., *Cirratulus* sp., and *Exogone clavator* are typical *r*-selected taxa that thrive in disturbed, high-energy shallow habitats, characterized by traits that enhance their resilience under frequent disturbance (Gambi and Giangrande, 1985; Tin et al., 2021). Other species, including *Schistomeringos* sp. and *Leodamas* sp., although not restricted to shallow habitats, exhibit moderate alignment with soft-sediment traits typical of shallow habitats (Nasi et al., 2018; Rousou et al., 2023). These taxa benefit from the heterogeneous microhabitats created by shallow water habitats like seagrass beds and coarser substrate. Intermediate zones hosted species such as *Magelona capensis* and *Lumbrineris latreilli*, which were more prominent in this depth band and exhibited traits suited to transitional sediments, including burrowing and sub-surface feeding behaviors (Ribeiro, 2023; Joseph et al., 2021). In contrast, deeper, mud-rich zones were dominated by *Nephtys* sp., capitellids, and *Paralacydonia weberi*, which displayed deep-burrowing mobility and tolerance to low-oxygen, organically enriched conditions (Borja et al., 2010; Fauchald and Jumars, 1979; Jayachandran et al., 2019, 2020, 2024; Jumars et al., 2015). Such traits enable long-term exploitation of resources in low-oxygen, stable sediments. Although not strictly confined to individual zones, these species are emphasized due to their ecological functions and trait expressions, which align with prevailing environmental filters (Joydas et al., 2023; Levin and Gage, 1998; Montiel et al., 2011).

Species richness and diversity were highest in shallow zones and declined with increasing depth (Joydas et al., 2011; Tselepides et al., 2000). Similar trends were reported in the southern Red Sea (Farasan Islands), where peak macrobenthic diversity at inshore sites was driven by opportunistic polychaetes and bivalves in nutrient-rich sediments (Ellis et al., 2017). In contrast, deeper zones exhibited lower diversity but high evenness, suggesting functional trait convergence under environmental stressors such as low oxygen and reduced habitat complexity. This filtering effect is consistent with patterns observed in the Oxygen Minimum Zone (OMZ) of the Oman margin, where hypoxic conditions (<0.3 ml/L) select for soft-bodied polychaetes tolerant of extreme conditions (Levin et al., 2000). Similar bathymetric patterns in polychaete zonation, tightly linked to sediment gradients and niche partitioning,

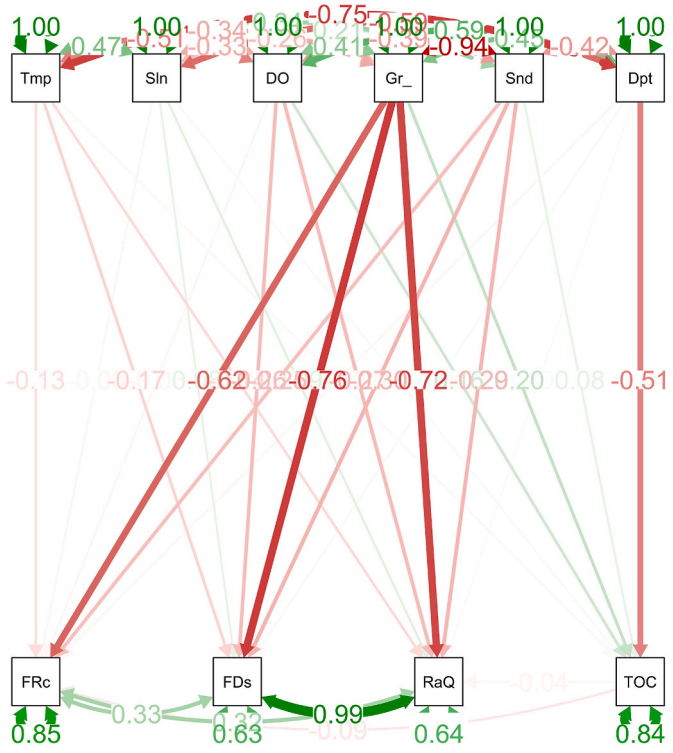

Fig. 7. Structural Equation Model (SEM) path diagram showing relationships between environmental variables and functional diversity indices (FRic, FDis, RaoQ). Line color indicates the direction of the relationship (green = positive; red = negative), and line thickness reflects the strength of standardized path coefficients. Only solid lines represent statistically significant paths ($p < 0.05$). Lighter (semi-transparent) lines indicate non-significant paths included in the model for completeness but not statistically supported. Gr_ = grain size (Φ); Tmp = temperature; Sln = salinity; DO = dissolved oxygen; Snd = sand; Dpt = depth; TOC = total organic carbon. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

have also been reported from Mediterranean soft-bottom habitats, notably in the Gulf of Salerno and Tyrrhenian Sea (Gambi and Giangrande, 1985, 1985, 1986, 1985; Gambi et al., 1983; Lorenti et al., 2011). Seagrass-associated species such as *Aricidea* spp. and *Syllis* spp. were abundant in shallow zones, supported by high oxygen levels, structural complexity, and food availability. The coarser, mobile sediments and disturbance from waves and currents favor smaller, surface-feeding polychaetes with short lifespans and high mobility (Rasha et al., 2022). Deeper habitats, characterized by low disturbance and finer sediments, supported larger-bodied burrowers adapted to stable conditions, with surface and sub-surface deposit feeders thriving in organically enriched substrates (Delfan et al., 2021; Sukumaran et al., 2025).

Functional diversity (FDis, RaoQ, FRic) varied across depth zones, with higher values in shallow and intermediate zones (Lefcheck, 2016; Mason et al., 2013; Mouillot et al., 2013). These elevated values are linked to habitat heterogeneity, and greater productivity (Diaz and Rosenberg, 1995; Goswami et al., 2017; Petchey, 2003; Tilman, 2001). Higher functional richness corresponded with greater dispersion and divergence, reflecting niche differentiation and reduced trait overlap (Cadotte et al., 2011; Ellis et al., 2017; Sobczyk et al., 2021; Villéger et al., 2008; Zhong et al., 2020). In contrast, lower FRic in deeper areas suggests underutilized resources and greater vulnerability to disturbance (Hengeveld et al., 2002). RLQ and fourth-corner analyses revealed depth-specific trait distributions, strongly influenced by sediment grain size and oxygen availability (Jayachandran et al., 2024). SEM analysis confirmed the indirect role of depth in shaping functional composition through sediment properties. Fine sediments (higher Φ) were associated with trait clustering and lower diversity (Bosco Gusmao et al., 2022), while coarse sediments (lower Φ) supported broader trait ranges (Chauvel et al., 2024). These findings are consistent with habitat templet theory, where stable, resource-limited habitats select for specialized traits, while variable environments support opportunists (Southwood, 1977; Townsend and Hildrew, 1994).

Trait convergence in deeper zones and divergence in shallower zones are consistent with theories of limiting similarity and physiological filtering (Fetzer et al., 2015; Mason et al., 2005). In deeper habitats, unrelated taxa such as *Nephtys* and capitellids exhibit similar burrowing and feeding traits, a case of convergent evolution. In shallow areas, coexisting species show distinct trait combinations, enabling niche partitioning and resource complementarity (Mouillot et al., 2011). Life-history strategies also followed depth-related patterns: *r*-selected traits (small size, short lifespan, high fecundity) dominated in shallow, disturbed zones, while *K*-selected traits (larger size, long lifespan, burrowing behavior) were more common in deeper, stable environments (Pianka, 1970; Southwood, 1977). Intermediate zones hosted a mix of both strategies, aligning with the intermediate disturbance hypothesis (Pappas et al., 2017; Rosli et al., 2018). Low functional redundancy in the Arabian Gulf polychaete community indicates that many key ecological functions are supported by single species, increasing vulnerability to biodiversity loss (Sukumaran et al., 2025). Loss of any functionally unique taxon could result in disproportionate ecosystem disruption, as few or no species are available to compensate (Pombo-Ayora et al., 2024; Solan et al., 2004). In more diverse systems, high redundancy provides resilience, but such 'functional insurance' is limited in the Gulf (Fetzer et al., 2015). These findings emphasize the importance of conservation strategies that account for both species and trait diversity. Protecting sediment heterogeneity, reducing anthropogenic impacts, and implementing depth-specific management plans are essential. Future studies should incorporate seasonal and hydrodynamic variability and larval supply.

5. Conclusions

This study reveals apparent depth-related shifts in environmental conditions and functional trait composition of macrobenthic polychaete communities in the Arabian Gulf. Among all variables, grain size (Φ) consistently emerged as the strongest ecological filter across zones. Shallow zones, characterized by coarser, oxygen-rich sediments, supported higher functional diversity, trait dispersion, and a broader range of life-history strategies. In contrast, deeper zones with finer, organic-rich sediments favored trait convergence, dominated by burrowing specialists adapted to low-oxygen, stable sediments. Multivariate analyses (RLQ, fourth-corner, SEM) confirmed that sediment properties were the primary drivers of functional composition, more so than water column variables. These findings highlight the pivotal role of benthic habitat structure in shaping the functional ecology of polychaetes. Given the high proportion of functionally vulnerable taxa and low redundancy observed, these systems may be especially susceptible to biodiversity loss. Conservation strategies in the Gulf should prioritize preserving sediment heterogeneity and minimizing anthropogenic disturbances, with targeted efforts across depth gradients. Future work should also incorporate seasonal dynamics, hydrodynamic regimes, and larval connectivity to better understand the functional resilience in this ecologically sensitive region.

CRediT authorship contribution statement

Paravanparambil R. Jayachandran: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Thadickal V. Joydas:** Sampling & Conceptualization, Writing – review & editing. **Seerangan Manokaran:** Writing – review & editing. **Jayanath Gopi:** Writing – review & editing. **Sudhanshu Dixit:** Writing – review & editing. **Mantodi Jima:** Writing – review & editing,

Visualization, Software, Formal analysis. **Karuppasamy P. manikandan:** Sampling, Writing – review & editing. **Mohamed Asharaf Thattathazhath:** Sampling, Writing – review & editing. **Premlal Panickan:** Sampling, Writing – review & editing. **Mohammed A. Qurban:** Writing – review & editing, Conceptualization. **Ali M. Qasem:** Writing – review & editing, Conceptualization. **Hamed Alghamdi:** Writing – review & editing. **Diego Lozano-Cortés:** Writing – review & editing.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT based on GPT-4 in order to improve language and readability. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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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.marenvres.2025.107373.

Data availability

Data will be made available on request.

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