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Exploratory patterns of functional traits and feeding guilds of benthic macroinvertebrates across coastal sites in Kampung Blekok, Situbondo, Indonesia

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ABSTRACT

Trait-based approaches can complement taxonomic assessments by describing ecological strategies of benthic organisms across coastal habitats. This study explored taxonomic composition, functional traits, feeding guilds, and sediment characteristics across six coastal sites in Kampung Blekok, Situbondo, Indonesia. Benthic macroinvertebrates were collected using standardized 25×25 cm quadrats, and functional composition was quantified using abundance-weighted biological traits analysis with fuzzy coding. Taxonomic and functional dissimilarities were evaluated using Bray–Curtis distance, while sediment characteristics were assessed using standardized Euclidean distance. Taxonomic composition differed markedly among sites, from complete dominance of *Nereis* at Site 1 to strong dominance of *Pirenella* at Sites 5 and 6. Functional profiles were generally dominated by epibenthic, free-living, mobile, and surface-modifying organisms, whereas feeding guilds showed greater spatial variation. Taxonomic and functional patterns showed moderate correspondence (Mantel $r = 0.517$, $p = 0.0222$), while sediment dissimilarity was weakly related to taxonomic ($r = 0.077$, $p = 0.396$) and functional patterns ($r = 0.122$, $p = 0.386$). These results indicate partial coupling between taxonomic and functional turnover, whereas the measured sediment variables did not clearly track biological variation. Given the absence of within-site replication, the findings should be interpreted as exploratory site-level patterns rather than causal relationships.

Keywords: benthic macroinvertebrates; biological traits analysis; feeding guilds; fuzzy coding; mangrove-associated coast; functional composition

INTRODUCTION

Tropical mangrove coastlines form spatially complex mosaics of vegetated sediments, tidal creeks, exposed mudflats, and human-modified shorelines. These connected habitats support benthic macroinvertebrates that contribute to organic-matter processing, nutrient cycling, sediment reworking, and energy transfer to fish, crustaceans, and shorebirds. Macroinvertebrate assemblages may vary considerably over relatively short distances because habitat structure, tidal exposure, sediment properties, and proximity to mangroves influence the availability of food,

shelter, and suitable living space. Studies in mangrove-associated systems have consequently reported spatial differences in both taxonomic composition and the relative expression of biological traits among mangrove forests, creeks, beaches, and adjacent mudflats (Hajializadeh et al., 2020; Meijer et al., 2021).

Conventional benthic assessments commonly emphasize taxonomic composition, abundance, richness, and diversity indices. These descriptors are essential for documenting biodiversity, but taxonomic identity alone does not fully explain how organisms acquire resources, occupy the sediment, move, or modify the seabed. Trait-based approaches complement taxonomic assessment by describing morphological, behavioral, and ecological attributes associated with organism responses and ecosystem processes. In marine benthic ecology, frequently applied traits include body size, feeding mode, living habit, mobility, sediment position, and bioturbation mode (Lam-Gordillo et al., 2020; de Juan et al., 2022; Beauchard, 2023).

Functional diversity is conceptually grounded in the variety, distribution, and relative expression of biological traits and ecological roles within an assemblage. Biological traits describe how taxa obtain food, move, occupy space, and interact with sediments, whereas ecological guilds group taxa that perform comparable functions, particularly similar modes of resource acquisition. Functional trait and guild composition therefore provides the empirical basis for interpreting functional diversity. However, an assessment of trait and guild patterns does not necessarily constitute a calculation of composite functional-diversity indices. Accordingly, the present study examines the underlying components of functional diversity trait modalities and feeding guilds rather than estimating functional richness, functional evenness, or functional divergence.

The relevance of this approach is also evident in the broader development of aquatic bioassessment. A recent bibliometric synthesis of 815 peer-reviewed publications identified functional diversity as one of six principal themes in aquatic bioassessment, together with bioassessment, biomonitoring, diatoms, water quality, and phytoplankton (Aida et al., 2026). The same synthesis characterized functional diversity as an area that remains comparatively underdeveloped and emphasized the growing need for trait-based assessments, standardized procedures, and expanded trait databases for poorly studied aquatic taxa. These priorities are especially pertinent to tropical coastal ecosystems, where functional information is less complete than in well-studied temperate regions.

The reliability of trait-based assessment depends on transparent definitions, consistent modality classifications, and documented coding decisions. Fuzzy coding is particularly useful because a taxon may express more than one modality within a trait, such as using several feeding modes or occupying more than one sediment position. The New Zealand Trait Database (NZTD) provides a standardized framework for shallow-water marine benthic invertebrates and compiles trait information using explicitly defined modalities and documented sources (Lam-Gordillo et al., 2023). Although developed for New Zealand taxa, its standardized terminology can be applied as an operational framework to other regions when taxon-specific information is verified using peer-reviewed literature and all extrapolations are reported transparently.

Sediment properties provide an important environmental context for interpreting benthic functional composition. Grain-size fractions influence burrowing, attachment, locomotion, tube construction, and the vertical position of organisms within sediments. Sediment organic carbon represents a potential food resource for deposit feeders and detritus-associated consumers, although high organic enrichment may also alter sediment oxygen conditions. Consequently, spatial variation sediment characteristics may coincide with differences in feeding guilds, sediment position, mobility, and bioturbation strategies (Gusmao et al., 2022; Shi et al., 2023; Han et al., 2024).

Trait-based studies of tropical mangrove-associated macroinvertebrates remain limited compared with conventional taxonomic surveys. In Indonesia, macrozoobenthos assessments in mangrove ecosystems have mainly emphasized community composition, diversity indices, and bioindicator applications (Retnaningdyah et al., 2022). Kampung Blekok, Situbondo, contains mangrove-associated sediments, open coastal areas, tidal-channel influences, and sites near coastal infrastructure. This local heterogeneity offers an appropriate setting for an exploratory baseline assessment, while the absence of balanced within-site replication requires the study to focus on descriptive spatial patterns rather than causal or inferential comparisons.

This study therefore aimed to describe the taxonomic composition, abundance-weighted functional traits, and feeding guilds of benthic macroinvertebrates across six coastal sites in Kampung Blekok, Situbondo, Indonesia. It also examined descriptively whether differences in trait and guild profiles coincided with variation in sediment grain-size fractions and sediment organic carbon. By documenting trait sources, fuzzy-coding decisions, and site-level functional profiles, this pilot assessment provides a baseline for subsequent replicated studies and the future development of trait-based bioassessment in Indonesian mangrove-associated coastal systems.

MATERIAL AND METHODS

Study area and sampling design

The study was conducted in the coastal area of Kampung Blekok, Situbondo, East Java, Indonesia, in May-June 2026. Six coastal sites were selected purposively to represent the local range of mangrove-associated, open intertidal, river-influenced, and pier-influenced microhabitats (Fig. 1). Site 1(7°41’52.94”S; 113°55’18.37”E) represented an open mudflat near the estuary mouth, Site 2 (7°41’59.81”S; 113°55’17.11”E) an open mudflat located farther landward from the mouth, Site 3 (7°41’55.59”S; 113°55’23.87”E) an interior mangrove habitat, Site 4 (7°42’1.85”S; 113°55’22.75”E) a mangrove habitat adjacent to residential dwellings, a small-scale coastal processing facility, and an artificial channel that discharges domestic wastewater directly into the mangrove, Site 5 (7°41’57.16”S; 113°55’52.71”E) a site adjacent to settlement, and Site 6 (7°41’49.92”S; 113°55’53.91”E) a site adjacent to a pier.

Sampling was conducted once at each site during low tide, producing six standardized site-level observations. The same quadrat dimensions, sediment excavation depth, sieve mesh size, preservation procedure, and sorting effort were applied at all sites. Because within-site replication was not available, the study was framed as an exploratory and descriptive baseline assessment. Site-level differences were interpreted as spatial patterns and were not used to infer causal effects of mangrove cover, pier proximity, or sediment characteristics.

Benthic macroinvertebrate collection

Benthic macroinvertebrates were collected within a 25 × 25 cm quadrat, a sampling-unit size recently applied to assess gastropod assemblages across mangrove-associated tidal habitats and tropical intertidal coastal structures (Chong et al., 2025; Ross et al., 2026). Organisms visible on the sediment surface and on associated substrates, including mangrove roots, woody debris, stones, shells, and other hard structures within the sampling unit, were collected manually. Sediment within the quadrat was then

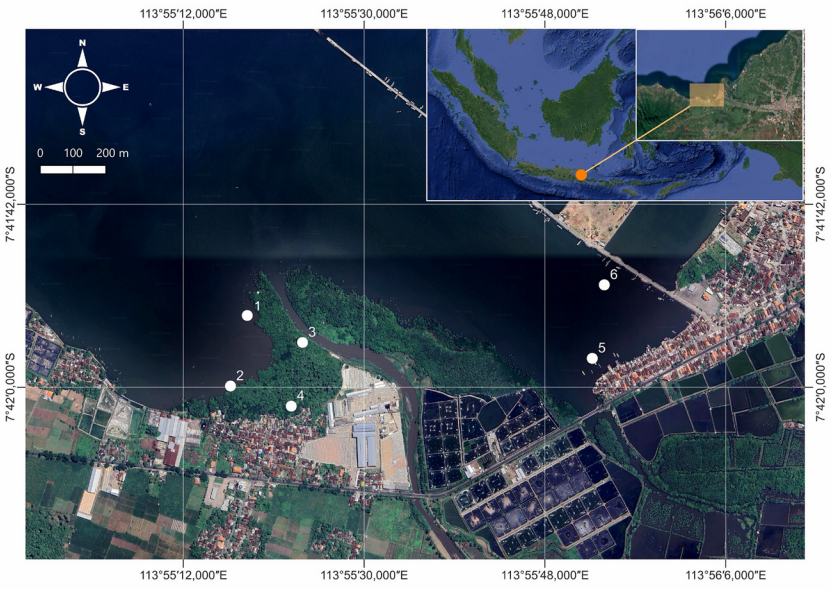


Figure 1. Map of the study area and sampling sites in Kampung Blekok, Situbondo, East Java, Indonesia

excavated to a standardized depth of 15 cm and washed through a 0.5-mm sieve, following general procedures for marine benthic macrofauna sampling (Eleftheriou, 2013; Hajializadeh et al., 2020; Pandya et al., 2021).

Material retained on the sieve was transferred into labelled containers and preserved in 70% ethanol. In the laboratory, samples were rinsed, sorted under a stereomicroscope, and counted. Empty molluscan shells, crustacean exuviae, unidentifiable fragments, and organisms outside the target macroinvertebrate groups were excluded from abundance calculations. Abundance was expressed as the number of individuals recorded within the standardized sampling unit at each site.

Taxonomic identification

Specimens were identified to the lowest practicable taxonomic level, preferably genus, using regional identification guides, taxonomic revisions, and peer-reviewed literature. Diagnostic characters were examined according to the relevant taxonomic group, including shell morphology and aperture characters in molluscs; carapace, appendage, and telson morphology in crustaceans; and prostomial, parapodial, and chaetal characters in annelids. Identifications that could not be supported reliably at genus level were retained at family level. Accepted names and current higher classification were checked using the World Register of Marine Species.

Sediment collection and analysis

A paired sediment sample was collected from the same location as the macroinvertebrate sample. Sediment from the upper 0–15 cm layer was retained for grain-size and organic-carbon analyses. Grain-size composition was determined by sieve analysis and expressed as the relative proportions of gravel, sand, and fine fraction. Because the available sieve data did not permit a reliable separation of silt and clay, the fine fraction was treated as a combined sediment component and no formal Shepard or Folk-based sediment class was assigned. Sediment organic carbon was determined using the Walkley–Black (1934) method and expressed as a percentage of sediment dry mass. Grain-size fractions and sediment organic carbon were used as site-level sediment descriptors in the exploratory dissimilarity analyses; no causal relationship with benthic composition was inferred.

Biological traits analysis framework

Functional composition was assessed using the matrix framework of biological traits analysis (BTA), which combines a site-by-taxon abundance matrix with a taxon-by-trait matrix to quantify the expression of biological characteristics within assemblages (Bremner et al., 2006). Trait terminology, modality definitions, and the 0-1 fuzzy-coding structure were based on the New Zealand Trait Database (NZTD) for shallow-water marine benthic invertebrates (Lam-Gordillo et al., 2023). Thus, BTA provided the analytical framework, whereas NZTD provided the operational trait nomenclature and coding scheme. Trait selection followed the study objective of describing resource use, movement, sediment occupation, and sediment modification (Lam-Gordillo et al., 2020) (Table 1).

Trait assignment and fuzzy coding

Fuzzy coding was used because a taxon may express more than one modality within a trait. Each modality received an affinity value between 0 and 1, where 0 indicated no affinity and larger values indicated stronger affinity. For each taxon, the modality values within a trait were normalized to a total of 1:

$$\Sigma_j f_{ij} = 1 \quad (1)$$

where: f_{ij} is the affinity of taxon i to modality j.

When a species or genus was represented directly in NZTD, the corresponding coding was adopted. When the recorded taxon was absent from NZTD, trait information was compiled from peer-reviewed ecological or taxonomic literature, prioritizing evidence at species level, followed by genus and family. All literature-derived assignments retained the trait names and modality boundaries used by NZTD. Each coding decision was documented with its source, taxonomic resolution, ecological justification, and level of confidence. A trait was recorded as missing when the available evidence was insufficient to support a defensible assignment.

Body-size coding was derived from the specimens collected in Situbondo rather than exclusively from literature-reported maximum sizes. For each taxon, measured individuals were allocated to the NZTD size classes, and the proportion of individuals in each class was

Table 1. Functional traits and modalities used in the analysis

Trait	NZTD modalities retained in this study
Bioturbation	Biodiffusor (BD); bioirrigator (BI); no bioturbation (NB); surface modifier (SM)
Body size	Small (0.5–<5 mm) (S); medium (5–20 mm) (M); large (>20 mm) (L)
Feeding mode / feeding guild	Deposit feeder (DF); filter/suspension feeder (FF); grazer/scraper (GS); omnivore (OM); predator (PR); scavenger/opportunist (SC); sub-surface deposit feeder (SSDF)
Living habit	Attached (ATT); burrower (BUR); free-living/surface crawler (FSC); parasite/commensal (PC); tube-dwelling (TD)
Mobility	Limited (LIM); mobile (MOB); sessile/attached (SES)
Sediment position	Attached (ATT); benthopelagic (BP); epibenthic (EPI); crevices, stones, and shells (CSS); deeper than 3 cm (D3); surface/shallow sediment <3 cm (S3)

used as the fuzzy affinity. Shell height was measured for gastropods, shell length for bivalves, maximum carapace width for crabs, and total body length for other taxa where appropriate. An individual measuring exactly 5 mm was assigned to the medium class to avoid overlap between classes.

Abundance-weighted trait composition

The taxon-by-trait matrix was combined with the site-by-taxon abundance matrix using an abundance-weighting procedure adapted from BTA. For each taxon, modality, and site, the weighted score was calculated as:

$$W_{ijk} = N_{ik} \times f_{ij} \quad (2)$$

where: W_{ijk} is the weighted score of taxon i for modality j at site k, N_{ik} is the number of individuals of taxon i at site k, and f_{ij} is its fuzzy affinity for modality j.

The total weighted score of each modality at a site was obtained by summing across all taxa:

$$W_{jk} = \Sigma_{i=1}\ S\ (N_{ik} \times f_{ij}) \quad (3)$$

where: S is the number of taxa recorded at the site.

Because total abundance differed among sites, modality scores were converted to within-trait percentages:

$$P_{jk} = [W_{jk} / \Sigma_{j=1}{}^{m}\ W_{jk}] \times 100 \quad (4)$$

where: P_{jk} is the abundance-weighted percentage expression of modality j at site k, and m is the number of modalities within the corresponding trait.

These percentages describe the proportional expression of trait modalities in the assemblage and should not be interpreted as mutually exclusive percentages of individuals when taxa have affinities to multiple modalities.

Taxonomic, functional, and sediment dissimilarity analyses

Site-level taxonomic composition was represented by the taxon-abundance matrix, while functional composition was represented by the abundance-weighted trait and feeding-guild matrix. Bray-Curtis dissimilarity was calculated separately for the taxonomic and functional matrices (Bray & Curtis, 1957). Hierarchical clustering was subsequently performed using group-average linkage (UPGMA; Sokal & Michener, 1958). Clustering analyses were conducted in R (version 4.4.1) through the RStudio environment.

Sediment characteristics were represented by gravel fraction, fine sediment fraction, and sediment organic carbon. Sand was not included in the multivariate sediment matrix because sediment fractions were compositional and sand was mathematically dependent on gravel and fine fractions. To account for differences in variable ranges, gravel, fine fraction, and organic carbon were standardized to z-scores prior to analysis. Euclidean distances were then calculated among sites, followed by group-average hierarchical clustering.

Cophenetic correlations were calculated for the taxonomic, functional, and sediment dendrograms to evaluate how well each clustering solution represented its underlying dissimilarity matrix. These correlations were not interpreted as independent evidence of the ecological validity of the resulting clusters. Correspondence between taxonomic and functional Bray-Curtis dissimilarities was assessed using a Mantel test (Mantel, 1967). Two additional exploratory Mantel

tests were conducted to examine correspondence between taxonomic and sediment dissimilarities and between functional and sediment dissimilarities. Mantel tests used Pearson correlations and all available unique permutations. Given the small number of site-level observations (n = 6) and the absence of within-site replication, all Mantel tests were interpreted as exploratory assessments of matrix correspondence rather than confirmatory evidence of ecological relationships. Furthermore, the taxonomic and functional matrices were not statistically independent because functional composition was derived from taxon abundances weighted by trait affinities.

RESULTS AND DISCUSSION

Taxonomic composition

Taxonomic composition differed markedly among the six sites (Fig. 2). Site 1 consisted entirely of *Nereis*, whereas Site 2 was dominated jointly by *Austruca* and *Nassarius* (28.57% each), followed by *Nereis* (14.29%). Site 3 was dominated by *Cassidula* (50.00%) and *Austruca* (31.25%). Site 4 showed a more distributed assemblage, led by *Neritodryas* (30.00%), *Olivella* (20.00%), and *Gelasimus* (15.00%). In contrast, Sites 5 and 6 were both strongly dominated by *Pirenella*, which contributed 86.67% and 65.22% of their respective assemblages; *Nassarius* was the second most abundant taxon at Site 6 (30.43%). These differences formed the taxonomic basis for the subsequent Bray–Curtis dissimilarity analysis among sites.

The six sampling sites showed pronounced spatial turnover in benthic taxonomic composition despite occurring within the same coastal landscape. Site 1, an exposed mudflat close to the estuary mouth, was completely dominated by *Nereis*, whereas Site 2, also an open mudflat but located farther landward, supported a more heterogeneous assemblage dominated by *Austruca* and *Nassarius*. This contrast indicates that apparently similar unvegetated mudflats may support markedly different assemblages depending on their position within the estuarine–intertidal mosaic. Estuarine macrofauna can vary over relatively short spatial gradients because tidal inundation, current velocity, salinity variability, sediment mobility, and food retention change with distance from channels and estuary mouths (Ysebaert et al., 2003; van der Wal et al., 2017; Zhang et al., 2023). Mangrove–mudflat connectivity may further contribute to these differences, because the spatial relationship between intertidal flats and adjacent mangroves can influence benthic community structure beyond sediment properties alone (Meijer et al., 2021). Although these processes were not measured directly, they provide a plausible ecological context for the contrasting assemblages at Sites 1 and 2.

The complete dominance of *Nereis* at Site 1 also illustrates why taxonomic simplicity does not necessarily imply equally simple functional composition. The fuzzy-coded *Nereis* profile included benthopelagic and epibenthic positions,

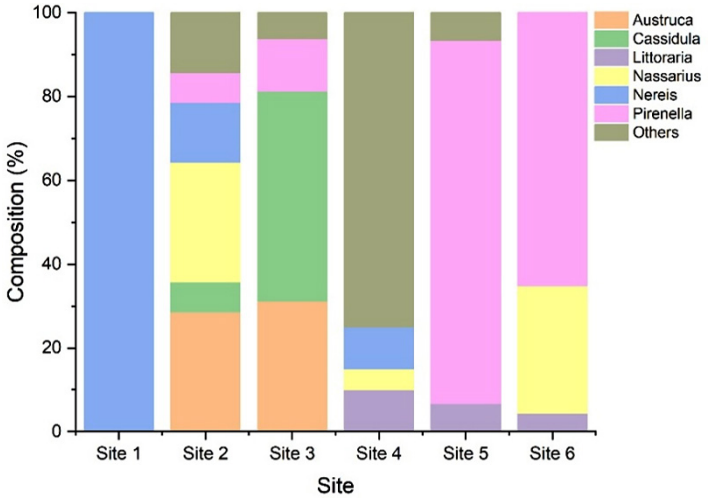


Figure 2. Relative taxonomic composition of benthic macroinvertebrates across the six sampling sites in Kampung Blekok
Note: Only the major taxa are shown individually, while less abundant taxa are grouped as "Others".

multiple feeding affinities, and both biodiffusion and surface modification, so a single dominant genus still contributed to several functional modalities. This highlights an important feature of Biological Traits Analysis: assemblages with low taxonomic richness may retain multiple ecological attributes when dominant taxa express several functional strategies (Bremner et al., 2006; Lam-Gordillo et al., 2020; Beauchard, 2023). Accordingly, the distinction between Sites 1 and 2 is better interpreted as a difference in both taxonomic structure and functional expression within two spatially distinct mudflat settings, rather than as a response to sediment composition alone.

A second major contrast occurred between the open mudflats and the mangrove-associated sites. Site 3, located within the mangrove interior, was characterized mainly by *Cassidula* and *Austruca*. Mangrove interiors differ from adjacent mudflats in several interacting characteristics, including root structure, canopy cover, hydroperiod, sediment retention, organic inputs, and oxygen dynamics. Studies directly comparing mangrove forests with adjacent tidal flats have shown that taxonomic composition may differ sharply between these habitats even where sediment characteristics alone do not explain the separation (Mattone & Sheaves, 2019). Likewise, Hajializadeh et al. (2020) and studies of mangrove habitat heterogeneity have demonstrated that macrofaunal trait composition varies among mangrove forests, creeks, and adjacent unvegetated habitats.

Functional trait and feeding-guild composition

Functional composition also varied among sites (Fig. 3). Body-size structure ranged from exclusively large-bodied organisms at Site 1 to exclusively medium-sized organisms at Site 6, while Site 5 was strongly dominated by the large size class (93.33%). Epibenthic organisms predominated at most sites, reaching 100% at Site 6, whereas Site 1 showed equal contributions of benthopelagic and epibenthic modalities. Free-living/surface-crawling organisms dominated all sites, although burrowers contributed more strongly at Sites 2–4.

Mobility was overwhelmingly represented by mobile organisms. Surface modifiers dominated the bioturbation profiles at Sites 2, 3, 5, and 6, whereas Site 4 exhibited a more heterogeneous combination of non-bioturbators (40.00%), surface modifiers (37.50%), biodiffusors (17.50%), and bioirrigators (5.00%). Feeding guilds showed greater spatial variation: Site 1 had equal contributions of deposit feeders, grazers/scrapers, predators, and scavengers/opportunists; deposit feeders dominated Sites 2, 3, 5, and 6; and Site 4 showed the broadest trophic mixture, with grazers/scrapers contributing the largest share (42.50%).

Habitat structure can also influence functional composition independently of simple taxonomic richness. Leung (2015) showed that variation in mangrove habitat heterogeneity was accompanied by changes in biological trait patterns. This is relevant to Site 3 because its interior-mangrove setting represents not merely a different substrate but a structurally different benthic habitat. Root systems and reduced hydrodynamic exposure may alter access to the sediment surface, burrowing space, detrital resources, and refuge availability, thereby changing which functional strategies are represented.

Site 4, located within mangrove habitat but adjacent to both residential dwellings and a small-scale coastal processing facility, exhibited the broadest combination of feeding and bioturbation modalities. Grazers/scrapers, deposit feeders, filter/suspension feeders, predators, and scavengers were all represented, as were surface modifiers, biodiffusors, bioirrigators, and non-bioturbators. This functional heterogeneity may reflect the intersection of mangrove structural complexity with a more modified coastal edge. Studies from Indonesia have shown that mangrove macrozoobenthos respond to differences in vegetation condition, water quality, land use, and anthropogenic pressure. Retnaningdyah et al. (2022) reported substantial differences in macrozoobenthic diversity among restored and reference mangrove ecosystems in East Java, while work in the mangrove-fringed Segara Anakan lagoon demonstrated marked spatial and temporal variation under long-term anthropogenic influence (Nordhaus et al., 2009).

Sediment characteristics and organic carbon

Sediment composition varied among the six sites, although sand represented the dominant fraction at all locations (Fig. 4). Sand content was highest at Site 3 (approximately 86%) and Site 5 (81%), whereas lower proportions occurred

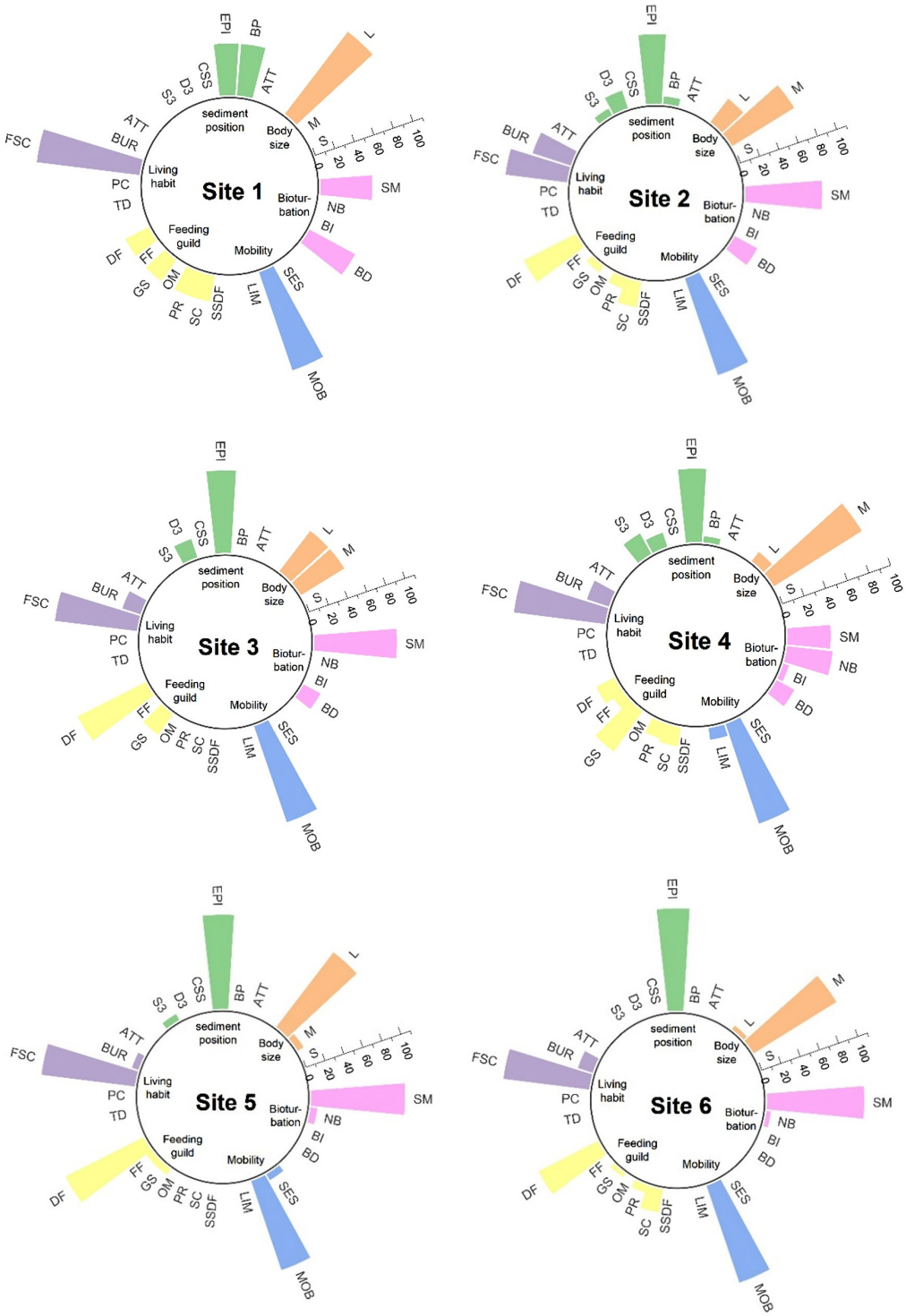


Figure 3. Abundance-weighted functional trait and feeding-guild composition of benthic macroinvertebrates across the six sampling sites in Kampung Blekok. Bar length represents the relative contribution (%) of each trait modality within its corresponding trait group. Trait abbreviations are provided in Table S1, while taxon-level fuzzy coding and supporting sources are provided in Supplementary Table S1.

at Site 2 (49%) and Site 6 (57%). Fine material showed the opposite pattern, reaching its highest proportion at Site 2 (approximately 41%) and Site 6 (33%), while Site 4 contained the lowest fine fraction (approximately 5%). Gravel generally represented a minor component, except at Site 4, where it accounted for approximately 21% of the sediment composition. Such spatial heterogeneity in grain-size composition is ecologically relevant because sediment structure

forms an important component of benthic habitat variation in intertidal and coastal systems (Bijleveld et al., 2025; Alves et al., 2024).

Sediment organic carbon also varied among sites (Fig. 4B). Site 4 showed the highest organic carbon content (3.84%), substantially exceeding the values recorded at the other sites. This site was located adjacent to an artificial drainage channel receiving domestic wastewater; however, the present study cannot establish whether this discharge was responsible for the elevated sediment organic carbon concentration. Organic carbon was lowest at Site 2 (0.51%), followed by Site 3 (approximately 0.76%), whereas intermediate values occurred at Sites 1, 5, and 6. Spatial differences in sedimentary organic carbon are relevant to benthic habitats because organic matter availability contributes to trophic resources and sediment biogeochemical conditions, while carbon accumulation commonly differs among sedimentary facies and hydrodynamic settings (Weissheimer and Colling, 2024; La Croix, 2025).

Sediment conditions were similarly heterogeneous, ranging from sand-dominated substrates with relatively low organic carbon to locations with greater fine-material accumulation or elevated organic carbon. Recent studies likewise emphasize that sediment grain size, mud content, organic matter, and related habitat properties can coincide with variation in taxonomic and functional characteristics of benthic assemblages, although the strength and direction of these relationships are system-dependent (Alves et al., 2024; Han et al., 2024; Nemani et al., 2024).

This organic-carbon pattern, however, should not be read as straightforward evidence that disturbance broadened the functional composition at Site 4. Disturbance can reduce, increase, or reorganize benthic diversity depending on intensity, frequency, habitat context, and the taxa involved. Site 4 was distinguished by an artificial channel that discharges domestic wastewater directly into the mangrove, and its markedly elevated sediment organic carbon relative to the other five sites is consistent with organic enrichment from this source: sewage-derived organic matter is efficiently retained in mangrove sediments and can substantially raise local organic carbon content (Clough et al., 1983; Li et al., 2023). Even so, the present study did not quantify discharge volume, nutrient loading, or vessel activity, and therefore the proximity of Site 4 to residential dwellings, small-scale processing activity, and this wastewater channel should be regarded as descriptive habitat context rather than a fully tested explanatory factor. What is clearer is that Site 4 combined a distinctive environmental setting with the widest observed range of feeding and bioturbation strategies.

The relatively high sediment organic-carbon concentration at Site 4 also warrants consideration of established biotic indices of organic enrichment, such as AZTI's Marine Biotic Index (AMBI; Borja et al., 2000) and the Infaunal Trophic Index (ITI; Word, 1978). These indices classify assemblages according to predefined ecological-sensitivity or trophic groups and summarize the resulting information into a diagnostic measure of ecological condition. Although conceptually related to biological-trait approaches, their purpose differs from that of the framework applied here. AMBI and ITI are primarily designed to assess ecological responses to organic enrichment or disturbance, whereas the trait-and-guild approach

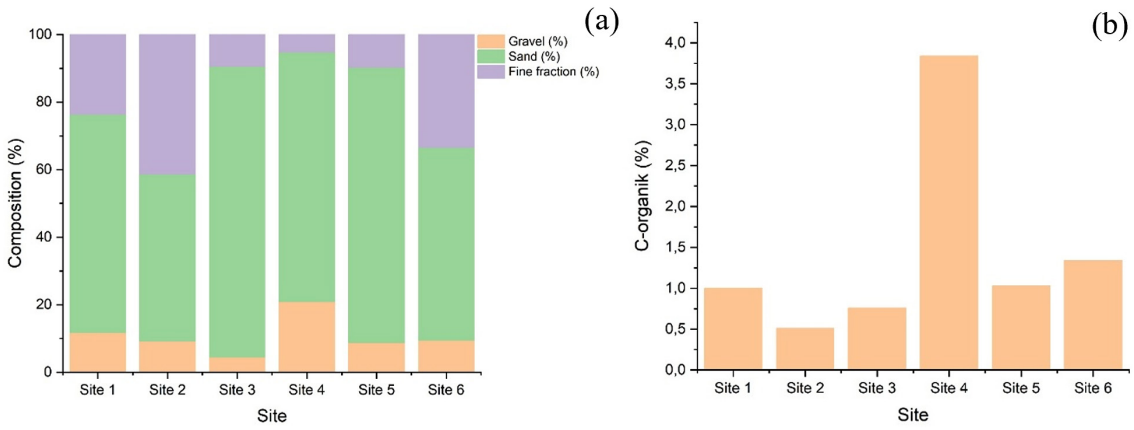


Figure 4. Sediment characteristics across the six sampling sites in Kampung Blekok
(a) Relative proportions of gravel, sand, and fine fraction; and (b) sediment organic carbon content

used in this study describes multiple dimensions of functional composition, including feeding, mobility, sediment position, and bioturbation. The approaches are therefore complementary rather than interchangeable. Future studies could apply AMBI or ITI alongside trait and feeding-guild profiles to evaluate whether the assemblage observed at Site 4 is also classified as indicative of organic enrichment using established biotic-index criteria. Such an analysis, particularly with greater spatial replication, could provide an independent line of evidence for interpreting the ecological significance of the relatively high organic-carbon concentration recorded at this site.

Exploratory clustering and correspondence among taxonomic, functional, and sediment characteristics

Hierarchical clustering revealed distinct but partly comparable site-grouping patterns among the taxonomic, functional, and sediment datasets. Taxonomic clustering (Fig. 5a) grouped Sites 5 and 6 most closely, indicating the greatest similarity in taxonomic composition between these sites. Sites 2 and 3 also formed a distinct pair and subsequently joined the broader grouping at a higher level of dissimilarity. Site 1 remained clearly separated from most other sites, consistent with its assemblage being entirely dominated by a single genus. The taxonomic dendrogram showed a high correspondence with the underlying Bray–Curtis dissimilarity matrix, with a cophenetic correlation of 0.941.

Functional clustering (Fig. 5b) showed a broadly comparable pattern. Sites 5 and 6 again clustered closely, while Sites 2 and 3 also formed a relatively similar pair. Site 4 joined the broader grouping at a higher level of functional dissimilarity, whereas Site 1 remained the most distinct and joined the other sites last. The functional dendrogram also represented the underlying Bray–Curtis dissimilarity matrix reasonably well, with a cophenetic correlation of 0.797.

Sediment-based clustering showed a different site-grouping pattern (Fig. 6). Sites 1 and 6 formed the closest pair, while Sites 3 and 5 also clustered relatively closely. Site 2 subsequently joined the Site 1–6 grouping, whereas Site 4 remained the most distinct sediment site and joined the other sites last. The sediment dendrogram showed a high cophenetic correlation of 0.943, indicating a good representation of the underlying standardized Euclidean distance matrix.

Comparison among the dissimilarity matrices showed that taxonomic and functional patterns were more closely aligned with each other than with sediment characteristics. Taxonomic and functional Bray–Curtis dissimilarities showed a moderate positive correspondence (Mantel r = 0.517, p = 0.0222; 719 unique permutations), indicating that sites that were more dissimilar taxonomically also tended to be more dissimilar functionally. In contrast, sediment dissimilarity showed only weak correspondence with taxonomic dissimilarity (Mantel r = 0.077, p = 0.396) and functional dissimilarity (Mantel r = 0.122, p = 0.386). Thus, the taxonomic–functional correspondence observed across sites was not clearly paralleled by variation in the measured sediment characteristics.

Sites 5 and 6 provide a particularly informative comparison. Site 5 was located near residential development, whereas Site 6 was situated near a pier. Despite these different local settings, both sites were strongly dominated by Pirenella and clustered closely in both taxonomic and functional analyses. Their functional similarity was therefore largely associated with the dominance of the same genus, resulting in high representation of

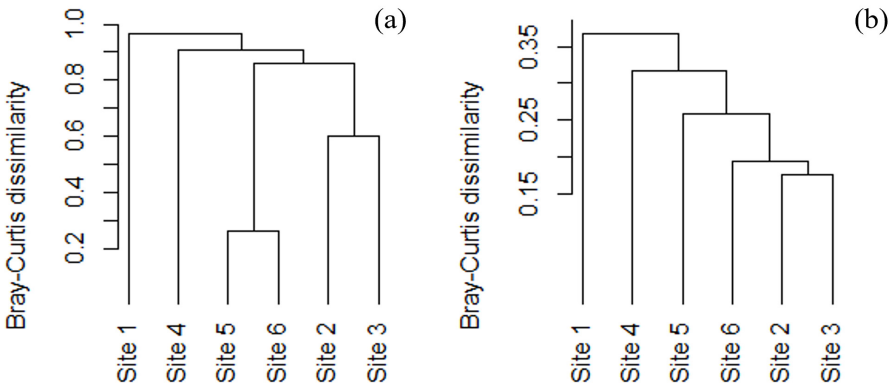


Figure 5. Taxonomic (a) and functional (b) clustering across the six sampling sites in Kampung Blekok

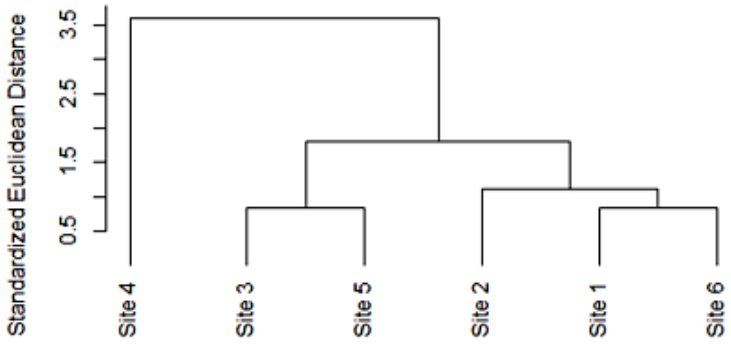


Figure 6. Sediment-based clustering across the six sampling sites in Kampung Blekok

epibenthic, free-living, mobile, deposit-feeding, and surface-modifying modalities. Pirenella is well adapted to intertidal soft-sediment environments and has been associated with deposit feeding and surface sediment processing in tropical intertidal habitats (Meziane & Tsuchiya, 2000; Kamimura & Tsuchiya, 2004; Reid & Ozawa, 2016; Yadav et al., 2025). Consequently, high abundance of Pirenella can exert a strong influence on the abundance-weighted functional profile of a site.

The similarity of Sites 5 and 6 is particularly interesting because they were not the closest pair in sediment characteristics. If sediment fractions and organic carbon were the principal determinants of community composition, a closer match between sediment and biological clustering might have been expected. Instead, sediment clustering grouped Sites 1 and 6 most closely, while Sites 5 and 6 remained most similar biologically. This mismatch indicates that the ecological similarity of Sites 5 and 6 cannot be explained simply by the measured sediment variables. Their shared position along a human-modified coastal margin may represent one possible contextual similarity, but the present data do not allow settlement influence or pier activity to be isolated experimentally.

The correspondence between taxonomic and functional composition was nevertheless clearer than the relationship of either biological dimension with sediment characteristics. Taxonomic and functional Bray–Curtis dissimilarities showed a moderate positive correspondence (Mantel r = 0.517), and the clustering analyses repeatedly grouped Sites 5–6 and, to a lesser extent, Sites 2–3. This indicates that taxonomic turnover was accompanied by functional turnover, but the relationship was incomplete. Such partial correspondence is expected because different taxa may share similar traits, while replacement of dominant taxa can sometimes produce substantial functional change. Trait-based studies increasingly emphasize that taxonomic and functional metrics provide complementary rather than interchangeable descriptions of benthic assemblages (Lam-Gordillo et al., 2020; de Juan et al., 2022; Gusmao et al., 2022). Gusmao et al. (2022), for example, showed that species composition and trait structure can change together along sediment gradients, but that trait-based measures may respond differently from taxonomic metrics.

The observed correspondence between taxonomic and functional patterns shouldn't be taken as independent evidence of an ecological relationship. That's because the functional matrix was itself derived directly from taxon abundances weighted by trait scores, meaning some degree of overlap between the two matrices is essentially built into the analysis from the start, rather than an independent empirical finding. In other words, the moderate Mantel correlation mainly reflects how similar the dissimilarity patterns are between two mathematically related matrices, rather than demonstrating a genuinely independent ecological link. Given the small number of unreplicated sites, this result is best interpreted descriptively rather than as strong statistical confirmation. Additionally, functional redundancy can't be quantified directly from this study design, and it shouldn't be inferred simply from this partial correspondence (Micheli & Halpern, 2005).

The sediment analysis adds an important counterpoint. Grain size and sediment organic matter are widely recognized as important determinants of benthic distribution because they influence sediment stability, pore-water conditions, burrowing capacity, organic-resource availability, and feeding mode. Studies in estuarine and intertidal systems have reported clear changes in both species and trait composition along sediment texture gradients (van der Wal et al., 2017; Gusmao et al., 2022; Zhang et al., 2023). In the Dutch Wadden Sea, for example, increasing grain size

was accompanied by a transition from small, deposit-feeding assemblages toward larger-bodied and more suspension-feeding communities (Gusmao et al., 2022).

In Kampung Blekok, however, the measured sediment pattern did not parallel the biological pattern. Sediment dissimilarity was only weakly related to taxonomic (r = 0.077, p = 0.396) and functional dissimilarity (r = 0.122, p = 0.386). This apparent decoupling is not unprecedented. Mattone and Sheaves (2019) found strong differences between tidal-flat and mangrove benthos that could not be attributed to sediment characteristics alone, and other mangrove studies have reported weak or inconsistent relationships between macrofauna and measured sediment biogeochemistry at small spatial scales. Such results emphasize that sediment is only one component of the habitat template and that local hydrodynamics, inundation regime, mangrove structure, dissolved oxygen, salinity variability, microtopography, food quality, and disturbance may interact to determine benthic assemblages.

This interpretation is especially consistent with the spatial arrangement of the six sites. Sites 1 and 2 differ primarily in their position relative to the estuary mouth; Site 3 represents an interior mangrove habitat; Site 4 combines mangrove vegetation with proximity to residential dwellings and small-scale coastal processing activity; Site 5 lies close to settlement; and Site 6 is associated with a pier. These categories encompass gradients in openness, tidal connectivity, vegetation structure, and human use that are not captured by gravel, fine fraction, and organic carbon alone. Seascape-scale studies have similarly shown that mangrove connectivity and spatial configuration can influence benthic communities independently of sediment characteristics (Meijer et al., 2021). Therefore, the weak sediment Mantel correlations should not be interpreted as evidence that sediment is unimportant, but rather that the measured sediment descriptors were insufficient to represent the full environmental heterogeneity among sites.

Considered jointly, these results point to a hierarchical interpretation of spatial variation in Kampung Blekok. First, the six sites supported clearly different taxonomic assemblages. Second, much of this taxonomic turnover was accompanied by changes in functional strategies, producing a moderate taxonomic–functional correspondence. Third, neither biological pattern was closely reproduced by the measured sediment characteristics. The observed spatial organization therefore appears more consistent with a heterogeneous coastal mosaic encompassing open mudflats, estuarine-mouth environments, mangrove interiors, settlement-associated edges, and pier-associated habitat than with a simple sediment-gradient model. This interpretation remains provisional because these habitat attributes were not quantified as independent predictors, but it provides a stronger ecological framework for understanding the site-level patterns.

Finally, these findings must be considered within the limitations of the sampling design. Each site was represented by one standardized site-level sampling unit, preventing separation of within-site variability from true differences among habitat settings. The Mantel comparisons therefore provide exploratory evidence of correspondence rather than tests of causal environmental control. Future sampling should incorporate replicated units within each habitat type and quantify tidal inundation, current velocity, salinity, dissolved oxygen, mangrove density and root structure, distance from the estuary mouth, and indicators of anthropogenic pressure. Such data would allow the present exploratory patterns to be tested formally and would help distinguish the relative contributions of sediment, seascape position, mangrove structure, and human disturbance to benthic taxonomic and functional organization.

CONCLUSIONS

Benthic macroinvertebrate assemblages in Kampung Blekok showed site-level variation in both taxonomic composition and functional characteristics. Taxonomic and functional dissimilarities showed moderate correspondence (Mantel r = 0.517, p = 0.0222), although this relationship was not statistically independent because functional composition was derived from the taxonomic abundance matrix. Sites 5 and 6 were particularly similar in both dimensions, associated with the strong dominance of *Pirenella*, whereas Site 1 remained distinct because of its complete dominance by *Nereis*. In contrast, sediment dissimilarity showed only weak correspondence with taxonomic and functional patterns, indicating that gravel content, fine fraction, and sediment organic carbon alone did not capture the full environmental heterogeneity among sites. The results support the value of combining taxonomic and

trait-based approaches for characterizing benthic assemblages in heterogeneous mangrove-associated coastal environments. However, because each site was represented by a single standardized sampling unit, these findings should be interpreted as exploratory spatial patterns rather than evidence of causal environmental effects. Future studies should incorporate within-site replication and a broader set of environmental variables to test these patterns more rigorously.

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