

Conservation prioritization of macrobenthic communities in subtropical bays: Insights from multidimensional beta diversity and community assembly processes

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ARTICLE INFO

Keywords:

Bay-Open Sea gradient
Beta diversity
Community assembly
Ecological uniqueness
Conservation prioritization
Marine macrobenthos
Coastal management

ABSTRACT

Understanding the spatial patterns of biodiversity and the underlying mechanisms of community assembly provides a scientific basis for the conservation and management of coastal ecosystems. Using macrobenthic communities from three subtropical bays and adjacent open waters in China, we assessed taxonomic, functional, and phylogenetic beta diversity (β_{sor}) and partitioned it into turnover (β_{sim}) and nestedness (β_{nes}) components. We employed variation partitioning (VPA), local contributions to beta diversity (LCBD), species contributions to beta diversity (SCBD), neutral community modeling (NCM), and the modified stochasticity ratio (MST) to identify key drivers of community differentiation and the relative roles of deterministic versus stochastic assembly processes. Results showed that β_{sim} dominated β_{sor} across all diversity dimensions. Spatial factors generally outperformed environmental variables in explaining beta diversity. Bay areas exhibited significantly higher ecological uniqueness in functional and phylogenetic composition, with deterministic processes dominating their community assembly, whereas stochastic processes prevailed in open waters. This study highlights that bay communities, shaped by environmental filtering, harbor unique functional trait combinations and evolutionary histories and should be assigned higher conservation priority. Integrating multidimensional beta diversity with community assembly mechanisms provides a quantifiable scientific framework for guiding conservation planning and marine protected area design in coastal ecosystems.

1. Introduction

Against the backdrop of rapid global environmental change and increasing challenges to conservation strategies, understanding biodiversity patterns and community assembly mechanisms has become a central focus in ecological research (Leibold et al., 2004). Traditional niche-based research has focused on deterministic processes, emphasizing how abiotic environmental filtering and biotic interactions shape community structure (Gravel et al., 2006). In contrast, neutral theory highlights the role of stochastic processes, proposing that random demographic events and dispersal limitation also fundamentally influence community composition (Hubbell, 2001; Rosindell et al., 2011). However, the relative dominance of deterministic versus stochastic processes and how they are regulated by disturbance regimes remain vigorously debated. Some studies indicate that stochastic processes dominate in relatively stable habitats, whereas deterministic processes driven by niche selection become more prominent in disturbed environments

(Chase, 2007). Conversely, other research suggests that environmental disturbance may enhance stochastic effects in community assembly by weakening species sorting (Fukumori et al., 2015). Moreover, disturbance may also maintain a relatively stable relative importance of community assembly processes while reshaping community beta diversity (Myers et al., 2015).

Biodiversity is a multidimensional concept that encompasses not only traditional taxonomic diversity but also functional diversity (reflecting differences in species' ecological roles) and phylogenetic diversity (reflecting differences in species' evolutionary histories). To comprehensively understand the distribution patterns of these different dimensions of diversity, they must be quantified across multiple spatial scales (Whittaker, 1960). Alpha diversity describes species richness and evenness within local habitats, whereas gamma diversity represents the species pool at the regional scale. As the key link between local and regional diversity, beta diversity captures spatial variation in species composition along environmental gradients, thereby providing critical

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insights into the underlying ecological processes (Baselga, 2010). Earlier studies of community assembly largely focused on taxonomic dimensions, but methodological advances have increasingly enabled the incorporation of functional traits and phylogenetic information into beta diversity analyses, thereby expanding our understanding of the mechanisms shaping biodiversity (Arnan et al., 2017). Because niche-based processes such as environmental filtering and dispersal limitation act directly on species' functional traits, functional beta diversity offers critical mechanistic insight into community structure and its spatial variation (Heino and Tolonen, 2017). Meanwhile, phylogenetic beta diversity reflects evolutionary divergence among species, and when traits exhibit strong phylogenetic conservatism, phylogenetic distances can serve as effective proxies for functional differences (Gerhold et al., 2015).

According to the framework proposed by (Baselga, 2010), beta diversity can be partitioned into two ecologically meaningful components: turnover (β_{sim}) and nestedness (β_{nes}). β_{sim} refers to spatial species replacement driven by environmental filtering or geographic barriers, whereas β_{nes} reflects systematic subset-superset patterns arising from species loss or gain along environmental gradients or across habitats (Legendre, 2014). Partitioning beta diversity into β_{sim} and β_{nes} components enables a more nuanced understanding of species distribution patterns and provides essential insights for biodiversity assessment and conservation planning (Socolar et al., 2016). For instance, high β_{sim} typically implies the need to conserve a greater variety of habitats to maintain regional diversity, whereas β_{nes} -dominated patterns suggest prioritizing species-rich core habitats (Hill et al., 2019). Similarly, functional and phylogenetic beta diversity can also be partitioned into their respective β_{sim} and β_{nes} components, allowing the assessment of multidimensional beta diversity responses and the exploration of their underlying drivers along ecological gradients (Li et al., 2021; Wu et al., 2021; Zhao et al., 2021). Therefore, β_{sim} and β_{nes} are complementary components of between-community differentiation, yet their relative contributions may shift depending on the strength of local conditions and regional processes.

In the context of multi-regional conservation planning, partitioning overall beta diversity into local contributions to beta diversity (LCBD) and species contributions to beta diversity (SCBD) (Legendre and De Cáceres, 2013) provides a quantitative basis for assessing the ecological uniqueness of each region and establishing scientifically informed conservation priorities. LCBD quantifies the unique contribution of a site to overall community differences within the study area, whereas SCBD identifies the key species that contribute most to overall beta-diversity. Generally, sites with high LCBD values harbor distinctive species assemblages and may possess greater conservation value, whereas species with high SCBD values often represent core taxa driving community differentiation and thus warrant special attention in conservation planning (Luiz et al., 2025). In recent years, studies examining LCBD and its environmental correlates have been conducted mainly in freshwater and terrestrial communities (Luiz et al., 2025; Dai et al., 2024; Hill et al., 2021), while comparable research in marine habitats remains unavailable. Moreover, studies investigating SCBD and LCBD based on phylogenetic and functional data are still very limited (Nakamura et al., 2020).

To date, research on multidimensional beta diversity patterns and community assembly mechanisms has been conducted primarily in freshwater ecosystems, such as streams (Li et al., 2023), rivers (Luiz et al., 2025), ponds (Hill et al., 2021), and lakes (Ge et al., 2021; Heino et al., 2022). In contrast, comparable research in marine ecosystems remains notably limited, partly due to sampling challenges and policy constraints (Jia et al., 2025). We anticipate that the assembly of marine communities may differ substantially from that of freshwater communities. First, physicochemical gradients (e.g., salinity, temperature, nutrients) in marine environments are often steeper (Giller et al., 2004), which may intensify environmental filtering. Second, the widespread occurrence of source sink dynamics in marine systems can sustain

species in unfavorable areas through continuous individual supply from source populations, thereby weakening the direct correspondence between species distributions and environmental conditions (Stegen et al., 2015). Collectively, these factors may result in beta diversity patterns and their underlying drivers in marine communities differing from those observed in freshwater systems (Kinlan and Gaines, 2003).

Bay marine ecosystems are semi-enclosed waters that connect terrestrial and open marine environments, typically characterized by distinctive hydrological features and complex biogeochemical processes (Cloern et al., 2016). As the macrobenthos in bays are primarily of marine origin, community composition typically varies from the bay mouth to the open sea (Alves et al., 2020). In our study area, environmental stress increases markedly along the gradient from open waters to the inner bay, manifested by decreasing salinity and, influenced by surrounding urban agglomerations, significantly elevated eutrophication levels (e.g., high concentrations of nitrogen, phosphorus, and organic pollutants) (Huang et al., 2025; Jia et al., 2025). This directional gradient in environmental stress results in a declining trend in species diversity from offshore waters towards the inner bay. Consequently, bay systems provide ideal natural gradients for investigating the spatial patterns of beta diversity and the mechanisms underlying their formation.

This study aims to address four core scientific questions: (1) For subtropical marine macrobenthic communities, is beta diversity in the taxonomic, functional, and phylogenetic dimensions primarily driven by β_{sim} or β_{nes} ? Are beta diversity and its components correlated across dimensions? Given the extensive spatial coverage and high environmental heterogeneity of the study area, we hypothesize that β_{sim} is the main source of beta diversity and that different dimensions exhibit complementary patterns. (2) What is the relative explanatory power of environmental and spatial factors for beta diversity and its β_{sim} and β_{nes} components across the three dimensions? Considering the environmental differences between bays and open waters, we predict that environmental factors will have stronger independent explanatory power than spatial factors. (3) Do LCBD values differ significantly between regions (bays vs. open waters) across different dimensions? Which species exhibit the highest SCBD in each dimension? If bay areas are more distinctive in their taxonomic, functional, or phylogenetic composition, they should be considered conservation priorities. (4) Do marine macrobenthic communities assemble in a non-random manner? We hypothesize that strong ocean currents enhance stochastic dispersal in open waters, leading to the dominance of stochastic processes. In contrast, in bays where environmental pressures (e.g., eutrophication, reduced salinity) are stronger, deterministic processes may play a greater role.

2. Materials and methods

2.1. Study area

The study area is located in eastern Zhejiang Province, China, encompassing Hangzhou Bay (HZB), Xiangshan Bay (XSB), Sanmen Bay (SMB), and the adjacent open waters (Open) (China Bay Records Editorial Committee, 1992). Situated on the southern margin of the Yangtze River Delta, the area is influenced by the East China Sea tidal-wave system, exhibiting typical characteristics of a macrotidal bay with complex hydrodynamic interactions (Sun et al., 2024). This area is also experiencing significant anthropogenic pressures, with substantial wastewater discharge from rivers and coastal cities exacerbating environmental pollution (Jiang et al., 2019). This background of coexisting natural and anthropogenic pressures makes it an ideal system for investigating the diversity patterns and underlying drivers of marine macrobenthic communities.

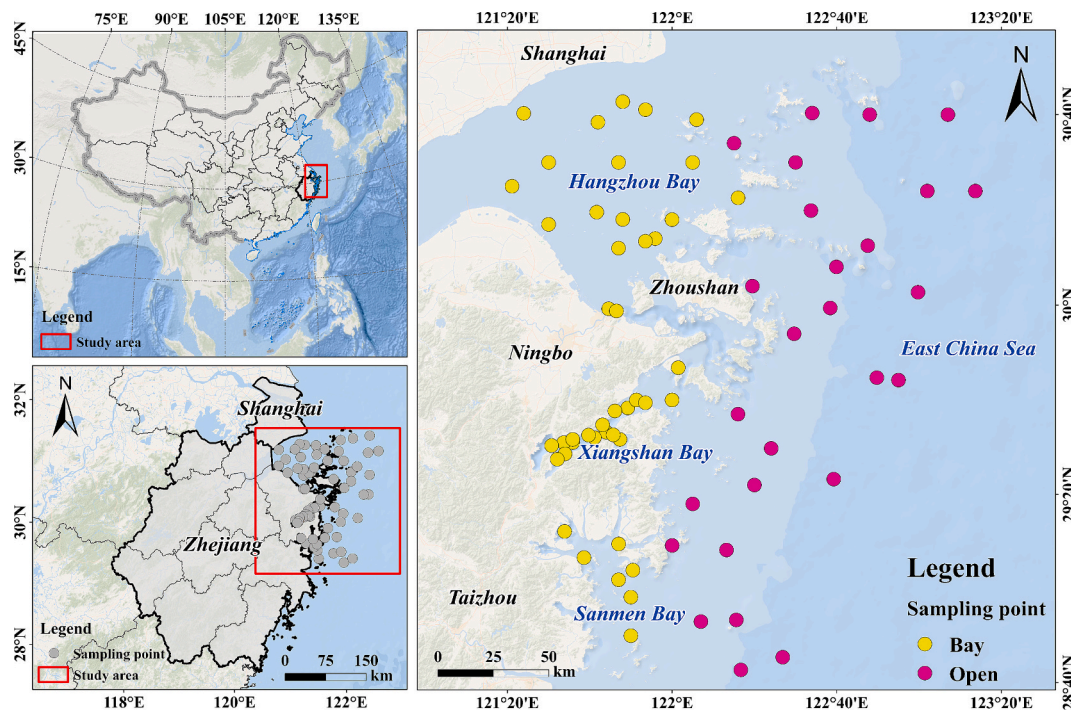


Fig. 1. Distribution of sampling stations for macrobenthic communities in the bays and open waters.

2.2. Macrobenthic communities sampling

Sampling was conducted at 71 stations along the eastern coast of Zhejiang Province from July to August 2020 (Fig. 1). Onboard sampling procedures strictly followed the “Technical Specifications for Marine Sediment Biological Surveys” (State Bureau of Quality and Technical Supervision of China, 2007). Quantitative sampling of macrobenthic communities was performed using a 0.1 m² stainless steel box corer. Triplicate samples were collected at each station. To enhance taxonomic identification robustness and reduce small-scale patch effects, two of the samples from each station were combined into a composite sample for subsequent analysis, while the remaining sample was used for sedimental measurements. The collected macrobenthos and associated residues were rinsed in the field, immediately preserved in 95% ethanol, and transported to the laboratory for identification. In the laboratory, preserved samples were stained with 1% Rose Bengal solution to facilitate sorting. All sorted macrobenthic individuals were morphologically identified under a stereomicroscope (Olympus SZ61, Japan) and classified to the lowest possible taxonomic level. We provide a species taxonomy table (Table S1) in the supplementary materials, which lists all detected taxonomic units along with their lowest identified taxonomic level.

2.3. Trait information and taxonomic levels

In this study, six biological traits and 25 trait modalities were selected and categorized for macrobenthos (Table S2). The selected traits modalities encompass key life-history characteristics (e.g., body length), resistance and recovery capacities (e.g., living habit, body protection, and mobility), and ecosystem functions (e.g., feeding mode and respiration type). These traits have been demonstrated to be effective indicators influencing the diversity and distribution patterns of macrobenthic communities (Dias et al., 2023; Martins et al., 2024). Functional traits for each species were quantified using fuzzy coding (Chevenet et al., 1994; Bremner et al., 2006). Based on the affinity of a species for a given trait modality, scores ranging from 0 to 3 were assigned, where 0 indicates no affinity and 3 indicates high affinity

(D'Alessandro et al., 2020; Dias et al., 2023). In the fuzzy coding procedure, we equalized the weights of trait categories to ensure that each functional trait contributed equally to the overall functional characterization. Trait information was obtained through direct observation of specimens, consultation of published literature (Fauchald, 1979; Jumars et al., 2015; Macdonald et al., 2010; Queirós et al., 2013; Yang and Sun, 1988; Yang and Wang, 1996), online databases (BIOTIC: <http://www.marlin.ac.uk/biotic/>; Marine Species Traits: <http://www.marinespecies.org/traits/index.php>; Arctic Traits Database: <https://www.univie.ac.at/arctictraits/>; Polytraits: <http://polytraits.lifewatchgreece.eu/polytraits/>), or communication with relevant experts.

In the absence of true phylogenetic information for macrobenthic species, we employed taxonomic distances based on the path length of the Linnaean taxonomic tree as a proxy for phylogenetic relationships. This approach has been shown to be a reliable surrogate for true phylogenetic structure (Li et al., 2021; Perez Rocha et al., 2018). We first carefully verified the taxonomic status of all species against the World Register of Marine Species (WoRMS) online database, and subsequently constructed a taxonomic tree using seven hierarchical levels (Kingdom, Phylum, Class, Order, Family, Genus, Species).

2.4. Environmental and spatial variables

Concurrent with macrobenthos sampling, environmental parameters were measured at each station. A total of 21 environmental parameters were selected to comprehensively reflect the potential influences of physical habitat characteristics and water quality conditions on macrobenthic community distribution. All environmental measurements strictly followed the “Specifications for Marine Monitoring” (State Bureau of Quality and Technical Supervision of China, 2007c, 2007d, 2007a, 2007b). The specific analytical methods were as follows: salinity, water temperature, depth, and dissolved oxygen were measured in situ using a YSI water quality meter (YSI, USA). Chlorophyll a (Chl-a) was determined by fluorescence spectrophotometry. Chemical oxygen demand (COD) was measured by the acidic potassium permanganate titration method. Total suspended solids (TSS) were determined gravimetrically. Phosphate (PO₄-P) was measured by the ascorbic acid-

reduced phosphomolybdenum blue method. Nitrite ($\text{NO}_2\text{-N}$) was determined by the diazotization method. Nitrate ($\text{NO}_3\text{-N}$) was measured by the zinc-cadmium reduction method. Ammonia nitrogen ($\text{NH}_4\text{-N}$) was determined by the hypobromite oxidation method. pH was measured using a pH meter. Reactive silica was determined by the silicomolybdenum yellow spectrophotometric method. Sulfide was measured by the methylene blue spectrophotometric method. Water content was determined by the drying method. Redox potential was measured by the potentiometric method. Sand content was determined using a Mastersizer 2000 laser particle size analyzer. Total organic carbon (TOC) was measured by the potassium dichromate oxidation-reduction volumetric method. Bacterial count was determined by the epifluorescence microscopy direct counting method. Dissolved inorganic nitrogen (DIN) was calculated as the sum of $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{NO}_2\text{-N}$. The eutrophication index (EI) was calculated as $\text{COD} \times \text{DIN} \times \text{DIP} \times 10^6 / 4500$. Detailed data for each environmental variable are provided in Table S3 in the supplementary materials.

Spatial variables were used as proxies for processes related to dispersal limitation. Distance-based Moran's eigenvector map (dbMEM) analysis using the dbMEM function were performed in the R package *adespatial* (Dray et al., 2025). Then, db-MEM variables with positive eigenvalues were retained as spatial predictors in subsequent constrained ordination analyses (Borcard et al., 2018). db-MEM can capture broad-scale spatial variation not explained by current environmental or historical factors, such as patterns generated by natural dispersal processes (Dalongeville et al., 2018). Specifically, db-MEM vectors with larger eigenvalues represent broader-scale spatial patterns in community structure, whereas those with smaller eigenvalues reflect finer-scale spatial structures (Borcard and Legendre, 2002). Through this process, we obtained 24 spatial factors for subsequent analysis.

2.5. Data analyses

2.5.1. Beta diversity decomposition, driver identification, and multi-dimensional correlation analysis

First, taxonomic beta diversity was calculated based on species occurrence data. Following the framework of Baselga (2010), total taxonomic beta diversity (β_{sor}) was decomposed into turnover (β_{sim}) and nestedness (β_{nes}) components using the Sørensen dissimilarity index (Baselga, 2010). This analysis was implemented using the *beta.pair* function in the *betapart* package. To assess the relative explanatory power of environmental and spatial factors for beta diversity and its components, we employed distance-based redundancy analysis (dbRDA) combined with variation partitioning (VPA). The specific procedure was as follows: first, the significance of the full model containing all environmental and spatial variables was tested using the *anova* function in the *vegan* package (Oksanen et al., 2018). If significant, backward selection was performed using the *ordstep* function (with 999 permutations) to identify environmental and spatial factors that significantly influenced each beta diversity component. Subsequently, dbRDA was performed using the *capscale* function, and VPA was conducted using the *varpart* function to calculate the unique and shared explanatory fractions of the significant factors. In addition, beta diversity was calculated not only for all stations combined but also separately for bays and open waters, in order to compare the patterns of beta diversity across different habitat types.

For functional beta diversity, we first calculated Gower distance based on the fuzzy-coded biological trait matrix using the *gowdis* function in the *FD* package to obtain a functional distance matrix among species (Laliberté et al., 2023). Subsequently, principal coordinate analysis (PCoA) was performed on this distance matrix, and the first two axes were retained as functional trait vectors. Finally, overall functional beta diversity and its turnover and nestedness components were calculated using the *functional.beta.pair* function in the *betapart* package, with the site-by-species matrix and the first two PCoA vectors as inputs. For phylogenetic beta diversity, we used taxonomic distance as a proxy

for phylogenetic relationships. The taxonomic distance matrix among species was calculated based on the path length of the Linnaean taxonomic tree using the *taxa2dist* function in the *vegan* package (Oksanen et al., 2018). Then, using the same PCoA and *functional.beta.pair* function as for functional beta diversity, we calculated total phylogenetic beta diversity and its turnover and nestedness components. After obtaining the functional and phylogenetic beta diversity matrices, we performed the same procedures of backward selection, dbRDA, and VPA as applied to taxonomic beta diversity, in order to identify the drivers and their relative importance for each dimension of beta diversity.

To explore the relationships among the components (i.e., β_{sim} and β_{nes}) of taxonomic, functional, and phylogenetic beta diversity, we applied Mantel tests. This analysis was performed using the *mantel* function in the R package *vegan*, with statistical significance assessed based on 9999 permutations. The Mantel statistic (r) ranges from -1 to 1 , measuring the correlation strength between two dissimilarity matrices, with larger absolute values indicating stronger correlations.

2.5.2. Quantification of ecological uniqueness based on LCBD/SCBD and hierarchical partitioning analysis

To quantify the ecological uniqueness of each station within the marine macrobenthic ecosystem, we calculated the local contribution to beta diversity (LCBD) for each station and the species contribution to beta diversity (SCBD) for each species using the *beta.div* function in the *adespatial* package (Legendre and De Cáceres, 2013). Subsequently, we calculated the functional local contribution to beta diversity (XLCBD) and the phylogenetic local contribution to beta diversity (PLCBD) using the *BD.extent* function in the *Dimensionality* package (Nakamura et al., 2020). Similarly, species contributions to overall functional beta diversity (XSCBD) and to overall phylogenetic beta diversity (PSCBD) were estimated based on this method. As the XLCBD, and PLCBD values did not follow a normal distribution (Shapiro-Wilk test, $p < 0.05$), we used the Wilcoxon rank-sum test to compare the differences in LCBD values across dimensions between bays and open waters. Considering the possible within-group correlation among the three bays, we further applied a linear mixed model (LMM) for validation. The analysis was performed using the *lmer* function in the *lme4* package (Bates, 2010). Detailed results are shown in Table S5.

Hierarchical partitioning analysis was conducted using the *glmm.hp* package to quantify the relative explanatory power of environmental variables and species richness on the various local contribution to beta diversity indices (Lai et al., 2023, 2022). In all analyses, predictor variables were standardized, and parsimonious models were constructed using backward selection to ensure model simplicity and comparability of parameter estimates.

2.5.3. Assessment of stochasticity in community assembly mechanisms

To assess the potential importance of stochastic versus deterministic processes in community assembly, we fitted the neutral community model (NCM) to species abundance and occurrence frequency data using nonlinear least squares (Sloan et al., 2006). The coefficient of determination (R^2) represents the overall goodness-of-fit of the model to the observed data, and the migration rate parameter (m) represents the dispersal rate at the community level. Model fitting was implemented using the R package *Hmisc* (Beck and Dupont, 2025). To further distinguish the relative influences of deterministic versus stochastic processes, we calculated the Modified Stochasticity Ratio (MST) using the *NST* package (Ning et al., 2019). This model employed abundance-weighted Jaccard dissimilarity with 1000 permutations. The MST uses 50% as a threshold: values below 50% indicate that deterministic processes dominate community assembly, whereas values above 50% indicate a greater role of stochastic processes. Finally, the Wilcoxon rank-sum test was used to compare MST values between bays and open waters.

All statistical analyses in this study were performed in the R studio (R Core Team, 2024).

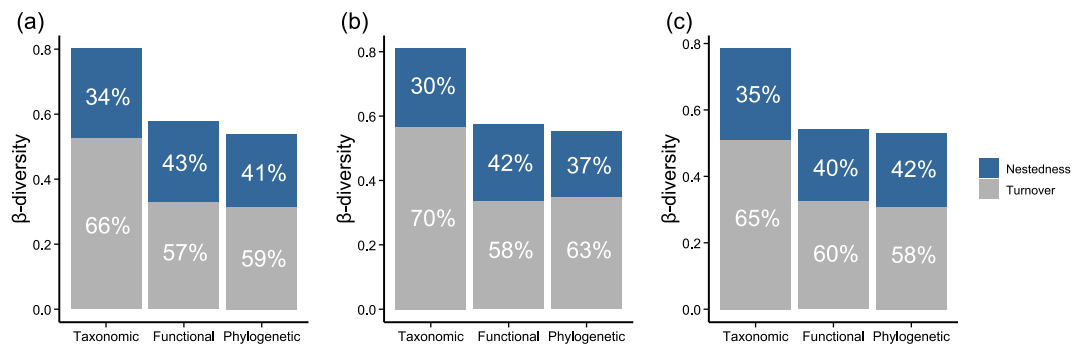


Fig. 2. Statistical summary of beta diversity components for macrobenthic communities across three dimensions (taxonomic, functional, phylogenetic). a) Meta-community; b) bay sites; c) open water sites. The numbers in each bar represent the relative proportions of total beta diversity partitioned into turnover and nestedness components.

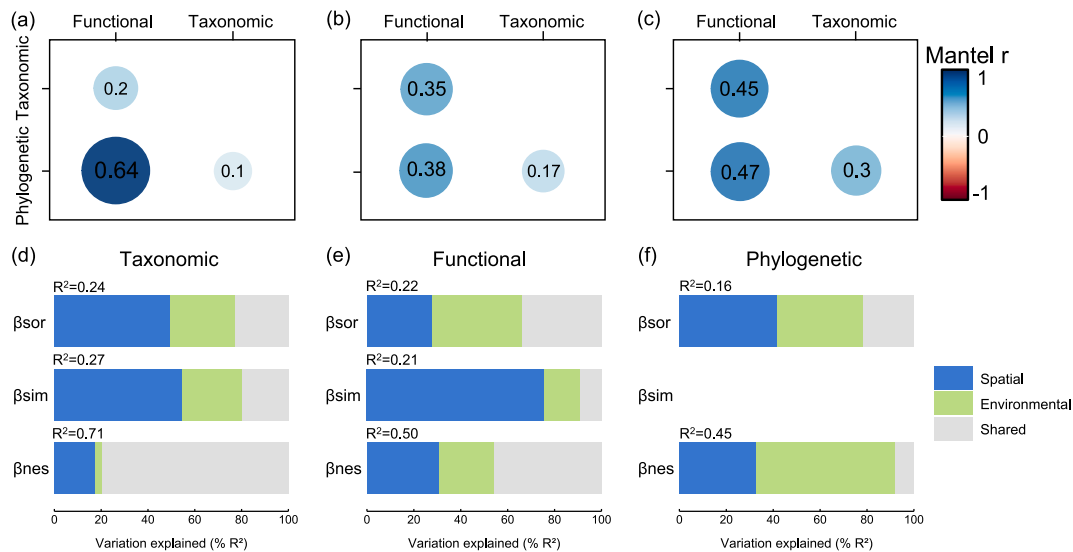


Fig. 3. Mantel correlations and variance partitioning results among multidimensional beta diversity components. (a–c) Mantel correlation matrices for β sor (a), β sim (b), and β nes (c) among different dimensions. All correlations were statistically significant ($p < 0.05$). Color intensity and numbers indicate the magnitude of the correlation coefficients. (d–f) Unique and shared explanatory fractions of environmental and spatial factors for taxonomic (d), functional (e), and phylogenetic (f) beta diversity components, based on R^2 .

3. Results

3.1. Macrobenthic community diversity components across taxonomic, functional, and phylogenetic dimensions

A total of 80 macrobenthic taxa were collected during the survey, belonging to 7 phyla, 11 classes, and 56 families (Table S1). Among them, 38 species were shared between bays and open waters, 19 were unique to bays, and 23 were unique to open waters. At the regional scale, the most widely distributed species were *Cossura dimorpha* and *Nemertea*. Environmental conditions differed markedly between bays and open waters. In terms of physical variables: the average water temperature in bays (27.84 °C) was 6.5 °C higher than that in open waters (21.30 °C), whereas the average salinity (20.54‰) was 11.7‰ lower than that in open waters (32.23‰). Dissolved oxygen in bays (6.83 mg/L) was higher than that in open waters (3.93 mg/L). Regarding nutrients: nitrate concentration in bays (0.60 mg/L) was higher than that in open waters (0.27 mg/L); the eutrophication index in bays (6.32) was substantially higher than that in open waters (1.01). Sediment sulfide was lower in bays (7.68 mg/kg) than in open waters (15.30 mg/kg).

Taxonomic beta diversity of macrobenthic communities was high (Fig. 2), with an overall β sor of 0.802 (Bay: 0.810; Open: 0.785). Functional and phylogenetic beta diversity were comparatively lower,

with a functional β sor of 0.579 (Bay: 0.575; Open: 0.541) and a phylogenetic β sor of 0.537 (Bay: 0.553; Open: 0.530). Across all three dimensions, beta diversity was primarily driven by β sim: taxonomic β sim was the highest, with an overall value of 0.525 (Bay: 0.566; Open: 0.509); functional β sim was 0.328 (Bay: 0.334; Open: 0.324); and phylogenetic β sim was 0.315 (Bay: 0.347; Open: 0.308). In contrast, the contribution of β nes was smaller: taxonomic β nes was 0.277 (Bay: 0.244; Open: 0.276), functional β nes was 0.251 (Bay: 0.241; Open: 0.217), and phylogenetic β nes was 0.222 (Bay: 0.206; Open: 0.222).

Mantel tests indicated that the correlations among the components of taxonomic, functional, and phylogenetic beta diversity, although relatively weak, were all statistically significant ($p < 0.001$; Fig. 3). Among them, the correlation between functional and phylogenetic β sor was the strongest ($r = 0.64$), followed by that between functional and phylogenetic β nes ($r = 0.47$).

3.2. Main drivers of macrobenthic community to Beta diversity

Based on the results of the anova function, all dbRDA models incorporating environmental and spatial variables, except for the model of the phylogenetic β sim component, were statistically significant ($p < 0.05$). The db-RDA models and the results of backward selection indicated that environmental and spatial variables jointly exerted a

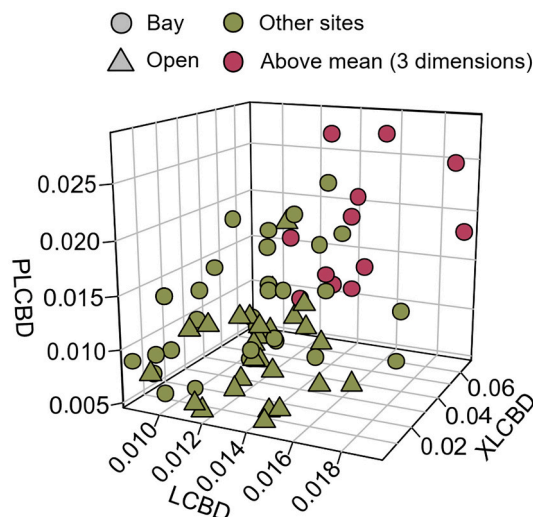


Fig. 4. Three-dimensional distribution of the local contributions to beta diversity for sampling stations across taxonomic (LCBD), functional (XLCBD), and phylogenetic (PLCBD) dimensions.

significant overall influence on the observed beta diversity patterns (Table S6). Among the environmental factors, nitrate, sulfide, water temperature, and chemical oxygen demand were identified as key variables influencing all three diversity dimensions. Regarding spatial factors, vectors representing broad-scale spatial structures were consistently identified as important predictors of beta diversity (Table S6).

VPA revealed that the proportions of unique effects attributed to environmental and spatial factors, as well as their shared effects, differed among the three dimensions of beta diversity and their respective components (Fig. 3). The total explained variation for all beta diversity indices ranged from 16% to 71%. For the unique effects, the independent explanatory power of spatial factors was generally greater than that of environmental factors. Furthermore, a considerable proportion of the explained variation was shared between the two sets of explanatory variables. However, these proportions varied substantially across different models, indicating that the responses of different beta diversity dimensions and components to the driving factors were distinct.

Specifically, for taxonomic beta diversity, the explanatory power of spatial variables for β_{sor} , β_{sim} , and β_{nes} (11.9%, 14.6%, and 12.2%, respectively) was higher than that of environmental variables. Among these, the total explained variation for β_{nes} was the highest (71%), but it was mainly attributable to the shared effects of environmental and spatial factors. For functional beta diversity, the independent explanatory power of environmental factors for the β_{sor} component (8.3%) was higher than that of spatial factors (6.0%); whereas for β_{sim} and β_{nes} , the independent explanatory power of spatial factors (16.2% and 13.7%, respectively) was higher than that of environmental factors (3.2% and 10.6%, respectively). For phylogenetic beta diversity, the unique explanatory rates of environmental and spatial factors for β_{sor} were relatively similar (spatial: 6.7%, environmental: 5.9%); whereas for β_{nes} , the unique contribution of environmental factors (26.7%) was substantially higher than that of spatial factors (14.8%).

3.3. Patterns of ecological uniqueness in sites and species

Analysis of local contributions to beta diversity showed that LCBD values ranged from 0.008 to 0.020, XLCBD from 0.001 to 0.070, and PLCBD from 0.005 to 0.029. By projecting the LCBD, XLCBD, and PLCBD values of each station into a three dimensional coordinate space, we identified 12 stations where the contribution values exceeded their

respective averages across all three dimensions (LCBD > 0.014, XLCBD > 0.014, PLCBD > 0.014) (Fig. 4; Fig. S1). These stations were all located within bays and are considered to harbor the most unique macrobenthic communities. Among them, the station with the most outstanding contribution values was located within Xiangshan Bay. Its community consisted of 13 species, among which *Phyllophorus ordinata*, *Perinereis nuntia*, *Atrina pectinata*, and *Cyclina sinensis* were rare species that occurred only at this station. Wilcoxon rank-sum tests revealed significant regional differences in XLCBD and PLCBD values (significantly higher in bay areas than in open waters), indicating that bay stations possess greater uniqueness in functional and phylogenetic composition (Fig. 5a–c). In contrast, no significant regional difference was detected for LCBD values. To avoid the potential influence of within-group correlation among the three bays, we further applied a linear mixed model for analysis (Table S5). The results showed that, after accounting for between-bay variation, when Bay and Open were included as fixed effects, the fixed effects for XLCBD and PLCBD were both significant ($p < 0.05$), whereas the fixed effect for LCBD was not significant ($p > 0.05$), consistent with the Wilcoxon test results. Hierarchical partitioning analysis showed that environmental variables and species richness together explained 42.4% of the variation in LCBD, 18.8% of the variation in XLCBD, and 39.4% of the variation in PLCBD (Fig. 5d–f, Table S7). Sulfide was significantly positively correlated with the local contribution values across all three dimensions. Station species richness (SR) was negatively correlated with PLCBD, indicating that stations with higher species richness tended to have more ordinary phylogenetic composition. Furthermore, indices related to eutrophication pollution (e.g., phosphate, nitrate) also showed significant negative correlations, suggesting that eutrophication processes reduce the uniqueness of a station's species composition.

The contributions of species to overall beta diversity differed among SCBD, PSCBD, and XSCBD (Fig. 5g–i). For both SCBD and PSCBD, the most important contributing taxa were *Sternaspis chinensis* and *Nemertea*, respectively, both of which were dominant taxonomic units across the entire study area. In contrast, for XSCBD, the most important contributors was *Raphidopus xinzhengi* (a species widely distributed along the Chinese coast north of the Taiwan Strait (Wang et al., 2026); in previous studies from this area, it was often identified as *Raphidopus ciliatus*), which are rare species with low occurrence frequency and abundance within the study area.

3.4. Relative importance of deterministic and stochastic processes in community assembly

To investigate the relative importance of deterministic versus stochastic processes in macrobenthic community assembly, we calculated the NCM and the MST. The results revealed a clear distinction in community assembly mechanisms between the bay and open waters (Fig. 6). The NCM fitting results indicated a much higher goodness of fit for the open waters ($R^2 = 79\%$) compared to the bay communities ($R^2 = 34.4\%$) (Fig. 6b, c). Concurrently, open waters exhibited a higher migration rate ($m = 0.046$) than bay communities ($m = 0.034$), suggesting more severe dispersal limitation for macrobenthos within the bays. The MST analysis further corroborated this pattern (Fig. 6d). MST values for bay communities were generally below 50%, indicating the dominance of deterministic processes in their assembly. In contrast, MST values for open waters communities exceeded 50%, suggesting that stochastic processes played a predominant role. The results from the NCM and MST analyses were mutually supportive, collectively confirming that deterministic processes had a stronger influence on bay communities, whereas the assembly of open waters communities was primarily governed by stochastic processes.

4. Discussion

The compositional patterns of species communities are the outcome

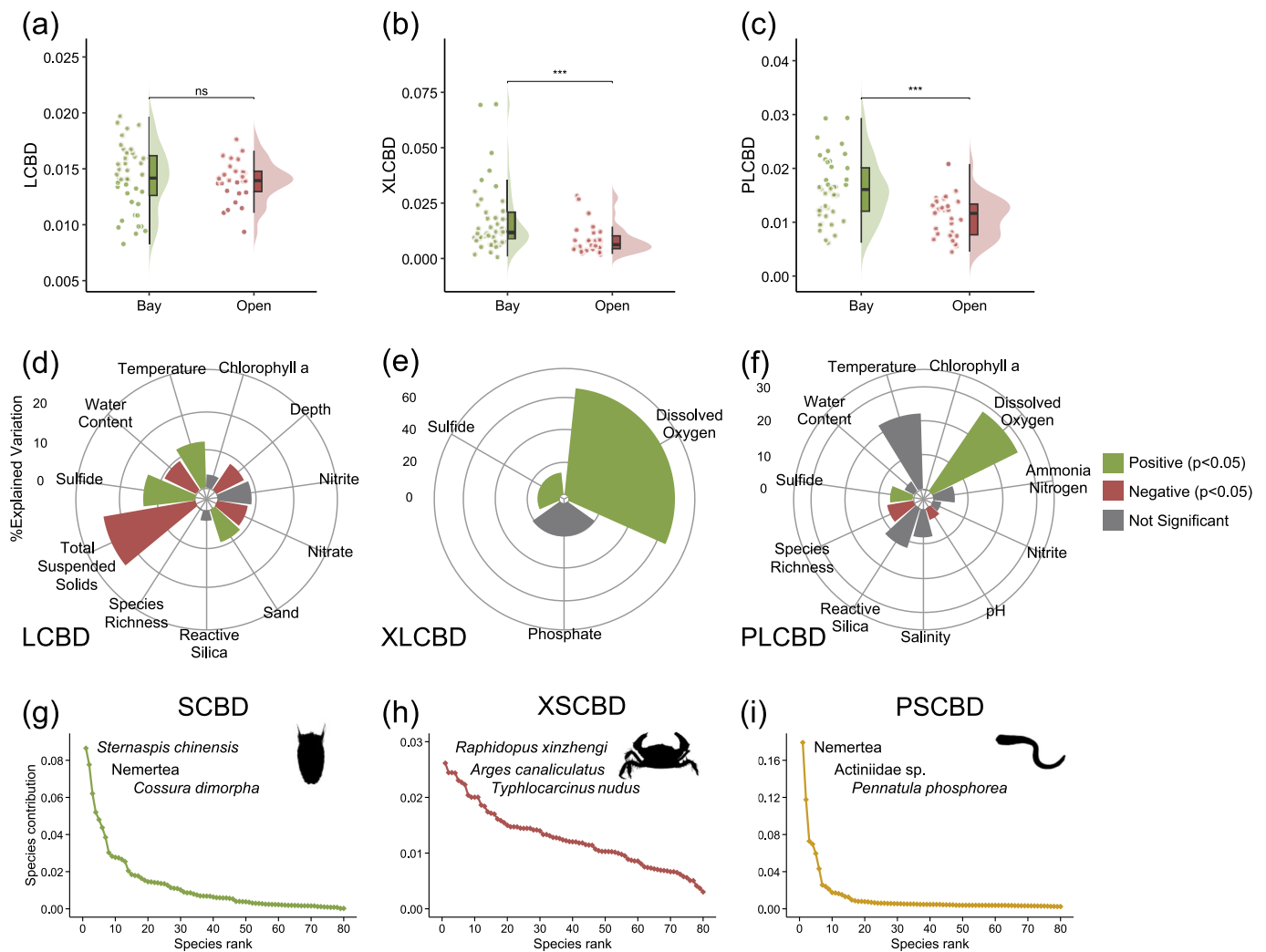


Fig. 5. Comparison of local contributions to beta diversity between bays and open waters, hierarchical partitioning of influencing factors, and species contribution rankings. (a–c) Comparison of differences in local contributions to beta diversity between bays and open waters. a) Taxonomic dimension (LCBD); b) Functional dimension (XLCBD); c) Phylogenetic dimension (PLCBD). In the boxplots, the center line represents the median and the box represents the interquartile range. Wilcoxon rank-sum test results: *** indicate $P < 0.001$, ns indicates not significant. (d–f) Independent and shared explanatory fractions of environmental variables and species richness for the three types of local contribution values, based on hierarchical partitioning models. d) Taxonomic dimension (LCBD); e) Functional dimension (XLCBD); f) Phylogenetic dimension (PLCBD). (g–i) Species contribution rankings to overall beta diversity. Each point represents a species, and the three species with the highest contributions are labeled in each panel. Silhouettes illustrate the representative morphology of the most important species in each group.

of long-term trade-offs between ecological adaptation and evolutionary processes (Ricklefs, 1987). By integrating multiple analytical approaches, this study elucidates the drivers of multidimensional beta diversity in macrobenthic communities in the bays and coastal waters. The results indicate that overall beta diversity was high in the study area, primarily driven by species turnover, with spatial factors being a key driver of macrobenthic beta diversity. In contrast, community distribution patterns in freshwater ecosystems are generally governed by environmental filtering (Wei et al., 2025; Hill et al., 2019; Jiang et al., 2024). In our study area, the spatial extent and geographic isolation of the three bays pose significant dispersal barriers for many macrobenthos. Previous studies have shown that spatial factors are often closely associated with processes such as dispersal limitation (Leboucher et al., 2020). Dispersal limitation promotes beta diversity by restricting gene flow and colonization (Fluck et al., 2020). Moreover, spatial variables can serve as effective proxies for unmeasured or spatially autocorrelated environmental factors (e.g., historical processes, unmeasured hydrodynamic conditions). Therefore, the strong explanatory power of spatial factors actually reflects the combined effects of dispersal limitation and spatially autocorrelated environmental variation.

Similar to findings from recent studies on the drivers of marine benthic communities, the independent explanatory power of environmental variables in this study was generally lower than that of spatial factors. This pattern has been reported in benthic community studies in Hangzhou Bay (Jia et al., 2025), Daya Bay (Rao et al., 2020), the Yellow River Estuary (Sun et al., 2026), and similar trends have also been observed in macrobenthic communities in the Wadden Sea (Sloots et al., 2025). Nevertheless, the contribution of environmental variables to the variation in beta diversity should not be overlooked. The study area exhibits a pronounced environmental gradient from semi-enclosed bays to open waters, with marked differences in sediment composition and salinity regimes, providing substantial scope for environmental filtering. Heterogeneity in environmental conditions among sites may impede the migration and exchange of individuals with differing adaptive capacities. This can promote ecological speciation—the process of species divergence driven by differential selection among distinct environments (Fluck et al., 2020). Thereby further amplifying compositional differences among communities. Among the various environmental factors, indicators associated with eutrophication (nitrate, phosphate, chemical oxygen demand) showed significant relationships with beta diversity.

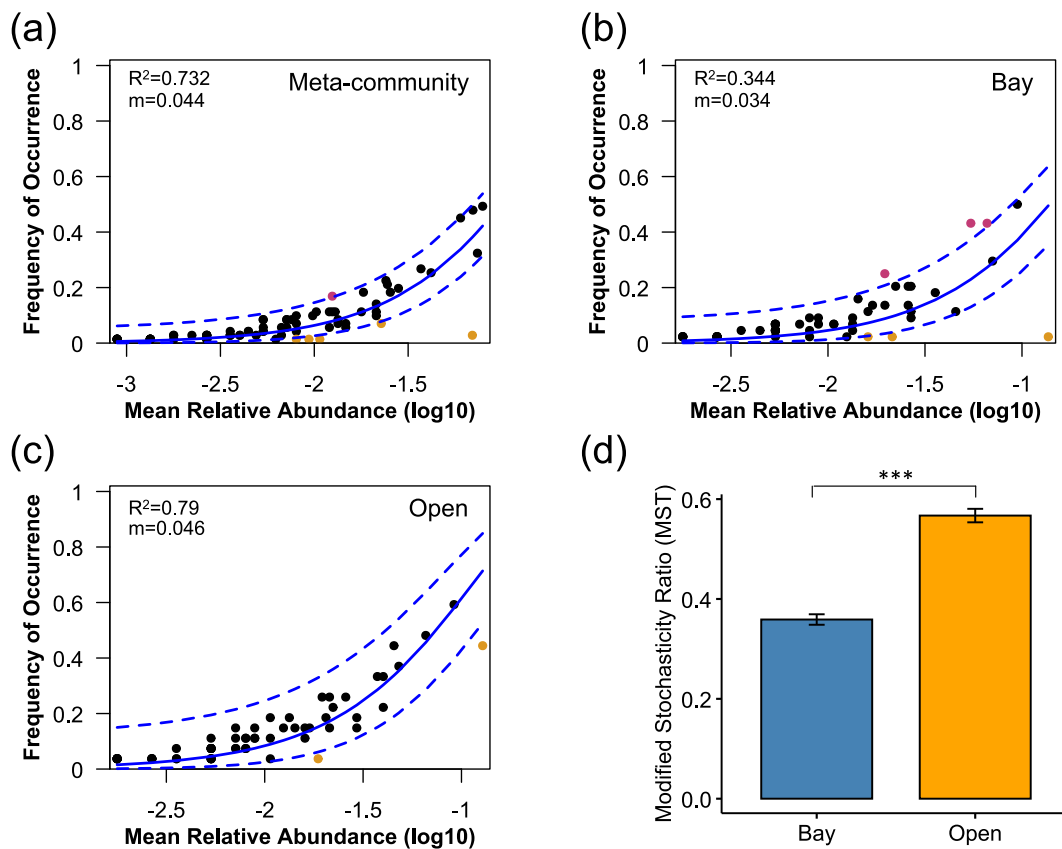


Fig. 6. Results of the NCM analysis. (a) Bay–open waters combined communities; (b) Bay communities; (c) Open waters communities; (d) Boxplot showing the percentage of MST (Wilcoxon rank-sum test results, $***P < 0.001$). In panels a–c, occurrence frequencies are colored red when above model predictions, orange when below predictions, and black when within the predicted range. Dashed lines represent the 95% confidence intervals of the model predictions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Influenced by anthropogenic activities such as coastal wastewater discharge, the study region exhibits a distinct spatial gradient in eutrophication (Jia et al., 2025). Such extreme nutrient gradients may prevent species adapted only to narrow pollution ranges from widespread distribution across the region, whereas tolerant species possessing opportunistic life-history characteristics (e.g., short lifespan, asexual reproduction) and unique phylogenetic lineages can survive (Huang et al., 2025), thereby driving compositional turnover in community structure.

Our results indicate that the correlations among taxonomic, functional, and phylogenetic beta diversity were slightly higher than those reported in previous studies on macrobenthos and benthic algae (Heino and Tolonen, 2017; Li et al., 2021; Wu et al., 2021), but lower than those found in fish studies (Chen et al., 2025; Villéger et al., 2013). This relatively low correlation suggests a complementary relationship among the three diversity dimensions within the study area, and relying on a single dimension as a surrogate for others may therefore be inadequate (Devictor et al., 2010). Consequently, in community ecology and biodiversity research, it is advisable to integrate taxonomic, functional, and phylogenetic dimensions to comprehensively capture the multifaceted nature of community structure (Li et al., 2021; Lin et al., 2024; Wei et al., 2025). Compared to taxonomic diversity, levels of functional and phylogenetic beta diversity were relatively low, indicating that, at the spatial scale of this study, the spatial variation in functional and phylogenetic composition was smaller than that in taxonomic composition. It is worth noting that the low level of functional beta diversity does not equate to effective functional redundancy, because our study area exhibits significant dispersal limitation, making it difficult for species to migrate among sites and achieve functional substitution. Therefore, the observed pattern of “high species turnover accompanied

by low functional turnover” in this study does not imply functional compensation or enhanced ecosystem stability. Instead, this pattern reflects that, under dispersal limitation, individual sites independently maintain similar functional structures but lack functional connectivity and complementarity with one another. In summary, to more comprehensively understand the composition and dynamics of biodiversity, conservation practices should not be confined to uniqueness at the species level; they must also consider uniqueness in the functional and phylogenetic dimensions (Heino et al., 2022). Conservation strategies for macrobenthic communities informed by a multidimensional beta diversity perspective can help more effectively identify areas and taxa of high ecological value or evolutionary representativeness, thereby enhancing the comprehensiveness and scientific basis of conservation actions (Mazel et al., 2018).

Although this study identified several key drivers, the high residual variation in the ordination models suggests that the environmental and spatial variables considered here are not the sole sources influencing beta diversity in the station communities. This finding is common in community studies relying on adjusted coefficients of determination (Li et al., 2021; Wei et al., 2025) and may stem from unmeasured factors such as priority effects, evolutionary legacies, and stochastic processes (Ge et al., 2021). To this end, the NCM and the MST we employed complement the results of VPA to some extent. The NCM results indicate that stochastic processes play an important role in structuring the macrobenthic communities in this marine area, which helps explain the high unexplained variation in the ordination models. Furthermore, the MST analysis revealed that deterministic processes dominated in the bay areas, which is consistent with our expectations. The gradient distributed environmental conditions within bays significantly shape the distribution patterns of macrobenthic communities and filter out a large

number of poorly adapted species (Meng et al., 2025; Zhou et al., 2024), thereby reducing the relative influence of stochastic processes on community assembly. Ultimately, only species that possess similar tolerance traits, enabling them to withstand extreme conditions and facilitate rapid population recovery, can survive and coexist in the local communities (Cavender-Bares et al., 2009). In contrast, the open water communities exhibited a stochastic process dominated assembly mechanism. This is because the offshore areas of eastern Zhejiang are significantly influenced by the Zhejiang-Fujian Coastal Current and the Yangtze River Diluted Water. Frequent and strong currents may transport species over long distances and intermittently remove locally dominant species, releasing space for competitively inferior species (Dial and Roughgarden, 1998), thereby weakening interspecific competition and creating vacant niches. Therefore, the open-water communities are likely composed of species that randomly colonize from the regional species pool.

Although studies have explored site-based conservation prioritization for freshwater macroinvertebrate communities using multidimensional metrics (Heino et al., 2022; Hill et al., 2021; Li et al., 2023), comparable research in bay and offshore ecosystems remains scarce. Therefore, a deeper understanding of the formation and maintenance mechanisms of marine beta diversity is crucial for elucidating community assembly processes and formulating scientifically informed strategies for protected area prioritization. In this study, the high overall beta diversity and species turnover indicate that each site contributes significantly to regional macrobenthic communities diversity, theoretically supporting the necessity for comprehensive protection across the entire sea area (Baselga, 2010). However, comprehensive protection is often impractical due to real-world resource constraints. Under such circumstances, concentrating conservation resources on sites and species with more unique ecological composition becomes a more operational strategy (Zhao et al., 2021). This study found that sites with higher LCBD values were primarily distributed in bays, with particularly prominent patterns in the functional and phylogenetic dimensions. This is mainly attributable to the gradient distributed environmental conditions within bays, which make deterministic processes dominant in community assembly, thereby selecting for taxa possessing tolerant traits adapted to extreme conditions and fostering communities that are highly unique in functional and phylogenetic composition (Nakamura et al., 2020). It should be emphasized, however, that the adaptation of these communities to extreme conditions does not imply immunity to intensified anthropogenic stressors such as hypoxia or physical habitat destruction. Traits that enable them to survive under chronic stress may become disadvantageous under rapid environmental change, and the loss of these unique communities would erode functional diversity and evolutionary heritage. Consequently, such areas hold higher value for regional biodiversity conservation (Zhao et al., 2021). In contrast, open-water sites generally had lower LCBD values. This is because ocean currents transport species over long distances, making community assembly more dominated by stochastic processes, thereby making it difficult to effectively maintain biodiversity in these areas through conservation interventions (Sloots et al., 2025).

On the other hand, SCBD helps identify key species that contribute most to variation in community composition. In this study, the species with high SCBD values differed markedly across dimensions: *Sternaspis chinensis* and Nemertea were prominent contributors in the taxonomic and phylogenetic dimensions, and they typically possess opportunistic life-history strategies and rapid generation turnover rates; in the functional dimension, *Raphidopus xinzhengi*, despite its limited distribution within the study area, exhibited the highest XSCBD contribution due to its distinctive functional traits (e.g., the arthropod-specific carapace morphology and high physiological tolerance). The conservation value of these species does not arise from their vulnerability, but from their important roles in ecosystem functioning (e.g., bioturbation, nutrient cycling). Their loss could lead to irreversible damage to the ecosystem. In the macrobenthic communities studied here, the high contribution

Table 1
Comparison of macrobenthic beta diversity patterns and community assembly processes across marine systems.

Study region	Climatic zone	Ecosystem type	Key findings	Source
Dutch Wadden Sea	North Temperate	Intertidal, subtidal	Species-based community assembly is primarily driven by stochastic processes, whereas trait-based assembly is governed by deterministic processes. Stochastic processes dominate community assembly. Environmental factors explain only a small fraction of community variation. In estuaries with low anthropogenic disturbance, benthic β -diversity is dominated by turnover; in those with high disturbance, turnover dominates in the dry season while both mechanisms act together in the wet season. Overall, turnover is the principal mechanism. Deterministic processes are the primary driver of macrobenthos and nematode communities. Taxonomic, functional, and phylogenetic β -diversity in both intertidal and offshore zones are dominated by turnover. Taxonomic, functional, and phylogenetic β -diversity are all dominated by turnover. Community assembly in bay areas is dominated by deterministic processes, while open waters are dominated by stochastic processes.	(Sloots et al., 2025)
Strait of Magellan, Yendegaia Fjord (Chile), Fildes Bay (Antarctica)	South Temperate	Bay		(Valdivia et al., 2021)
Mamanguape & Paraíba do Norte estuaries, Brazil	Tropical	Estuary		(Medeiros et al., 2016)
Araçá Bay, Brazil	Tropical	Bay		(Vieira et al., 2021)
Yellow River Delta, China	North Temperate	Intertidal, subtidal		(Wang et al., 2024)
Coastal Zhejiang, China	Subtropical	Bay, open waters		This study

species did not overlap across taxonomic, phylogenetic, and functional dimensions, indicating that beta diversity in different dimensions is driven by distinct species groups. This finding underscores that formulating conservation strategies requires the integrated application of multiple beta diversity frameworks (e.g., LCBD and SCBD) to account for both site uniqueness and the multidimensional functional roles of key species, thereby enhancing the systematicity and effectiveness of conservation measures (Liu et al., 2024).

It is worth noting that previous studies have not reached a consensus on how disturbance affects community assembly, and theoretical predictions may differ under other disturbance types or at different spatial scales (Table 1). The finding that deterministic processes dominate in bays whereas stochastic processes dominate in open waters is only applicable to the specific environmental gradient and spatial scale of this study. Therefore, future research is needed to further examine the effects of disturbance intensity and type on the relative roles of community assembly processes. In addition, this study used taxonomic distance as a proxy for phylogenetic structure. Although this approach has been widely used in previous studies (Bai et al., 2026; Li et al., 2021; Perez Rocha et al., 2018), its sensitivity may be limited in communities with large spatial scales or high evolutionary depth. Because taxonomic distance cannot reflect branch lengths or divergence times, it may lead to underestimation or bias in phylogenetic beta diversity (Miller et al., 2018; Molina-Venegas and Rodríguez, 2017). As molecular phylogenetic data for macrobenthic organisms continue to improve, future studies should attempt to validate the main conclusions of this study based on true phylogenetic trees.

5. Conclusion

We assessed the taxonomic, functional, and phylogenetic beta diversity of macrobenthic communities in bay and coastal waters using a multidimensional framework (incorporating turnover, nestedness and the local/species contributions to beta diversity). We simultaneously explored the roles of deterministic and stochastic processes in shaping these marine macrobenthic communities. Overall, the species turnover component consistently dominated the beta diversity across all three dimensions. The explanatory power of predictor variables for the variation in all aspects of beta diversity was relatively limited, with spatial variables explaining more variation than environmental variables. Regarding biodiversity conservation, we recommend assigning higher conservation priority to bay areas to guide conservation planning, because bays are often more distinctive in terms of environmental conditions and species composition. Furthermore, analyses based on stochasticity models confirmed that deterministic processes dominate in bays, whereas stochastic effects are more pronounced in offshore waters. In conclusion, our study underscores the importance of considering a wide range of ecological drivers and integrating multiple diversity dimensions into biodiversity research, conservation practice, and environmental assessment.

CRediT authorship contribution statement

Aoxiang Huang: Writing – original draft, Visualization, Validation, Formal analysis, Data curation, Conceptualization. **Shuyuan Huang:** Validation, Investigation. **Haodong Liu:** Validation, Investigation. **Shuting Jia:** Validation, Investigation. **Lin Zhang:** Validation, Investigation. **Qingxi Han:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grants No. 42076156) and the K.C. Wong Magna Fund in Ningbo University.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2026.115089>.

Data availability

The raw data supporting the findings of this study are available in the Figshare repository with the identifier doi:10.6084/m9.figshare.32320563.

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