



# Alpha and beta diversity patterns of gastropods communities in mangrove forests along the southeastern coast of China and their driving factors\*

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**Abstract** Understanding how biodiversity is distributed across environmental gradients is critical for effective conservation of coastal ecosystems. We investigated the  $\alpha$ - and  $\beta$ -diversity of gastropod communities along inner-to-outer transects in three mangrove-fringed bays, Dongzhaigang (Hainan), Yingluo Bay (Zhanjiang), and Quanzhou Bay (Fujian)—along China's southeastern coast, and identified the environmental drivers shaping these patterns. Results showed a consistent increase in  $\alpha$ -diversity (species richness and evenness) from inner to outer bay zones, with the lowest values in sheltered inner sites and highest near bay mouths.  $\beta$ -diversity decomposition revealed contrasting assembly mechanisms: community differences in Dongzhaigang and Quanzhou Bay were primarily driven by species turnover, indicating niche-based responses to natural gradients; in contrast, Zhanjiang exhibited strong nestedness, suggesting species loss likely linked to anthropogenic disturbance. Key environmental drivers varied among bays, including salinity, sediment organic carbon, clay content, and mangrove aboveground biomass. Site-specific environmental filtering not only shaped local  $\alpha$ -diversity but also determined whether spatial  $\beta$ -diversity was driven primarily by species turnover or nestedness. These findings highlight that biodiversity patterns in mangrove ecosystems are shaped by both natural gradients and human pressures, with context-dependent drivers. We propose that integrating  $\alpha$ -diversity with turnover/nestedness components of  $\beta$ -diversity can improve ecological assessments of mangrove health. Such metrics hold promise for guiding site-specific conservation, informing restoration design, and supporting national blue carbon and coastal resilience initiatives under the UN Decade of Ocean Science for Sustainable Development.

**Keyword:** mangrove; coastal bay; gastropod;  $\alpha$  and  $\beta$  diversity; environmental gradient

## 1 INTRODUCTION

Marine biodiversity is fundamental to sustaining ecosystem functioning and human well-being (Stachowicz et al., 2007; Bernhardt and O'Connor, 2021; Rodrigues-Filho et al., 2023). However, in recent decades, coastal ecosystems worldwide have been increasingly threatened by overfishing, habitat loss, pollution, climate change, and other stressors (Cui et al., 2018; Lin and Yu, 2018; Ani and Robson, 2021; Li et al., 2022b). The United Nations has designated 2021–2030 as the Decade of Ocean Science for Sustainable Development, promoting

science-based management and emphasizing the protection and restoration of coastal ecosystems (Ryabinin et al., 2019; Guan et al., 2023). However, the effective protection, restoration, and management

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of ecosystems require detailed and comprehensive baseline data.

The southeastern coastal regions of China represent globally significant marine biodiversity hotspots. However, due to rapid industrialization and urbanization, these habitats are becoming increasingly fragmented, with only some bays retaining contiguous distributions. Although ecologically and economically important, these bays are susceptible to anthropogenic pressures such as land-based pollution, aquaculture expansion, and coastal engineering (Yu et al., 2015). Moreover, their semi-enclosed hydrodynamic characteristics create spatial gradients in salinity, sediment properties, and nutrient distributions, which further shape the composition and structure of benthic communities (Little et al., 2017). Therefore, understanding the drivers of biodiversity patterns within these specific bay systems is critical for their effective conservation and management.

Mangrove forests, as unique coastal wetland ecosystems, provide critical nursery grounds and habitats for numerous marine species such as gastropod, crustaceans and fish, due to its dense root systems, high primary productivity and detritus upwelling (Sievers et al., 2023). Their biodiversity is central to maintaining ecosystem stability and resilience, supporting multiple ecosystem services including carbon storage, coastal protection, and fishery resources (Rahman et al., 2021; Sievers et al., 2023). Therefore, systematic research on mangrove-bay ecosystems is of paramount importance. Given that these ecosystems are primarily located in estuarine and bay areas, such research is crucial to reveal the coupling mechanisms between biodiversity and environmental gradients and to scientifically assess the impact of human activities on ecosystem integrity. This provides critical support for developing precise conservation strategies and sustaining coastal ecological security and human well-being.

Among benthic organisms, gastropods play critical roles in nutrient cycling, sediment stabilization, and food web dynamics in mangrove ecosystems (Koch and Wolff, 2002; Purnama et al., 2024), and they are widely used as biological indicators of ecosystem change (Salmo and Duke, 2010; Kabir et al., 2014; Sandaruwan et al., 2024). Previous studies have primarily focused on shifts in gastropod community composition during mangrove restoration, such as the increase in species richness and the shift from opportunistic to more specialized species with stand age observed in planted mangroves in the

Philippines and Vietnam (Salmo and Duke, 2010; Zvonareva et al., 2015; Salmo et al., 2017). Other studies have examined the responses of gastropod species to environmental variation, including salinity gradients and sediment properties (Reis et al., 2021; Pogado et al., 2022; Farahisah et al., 2023). However, the majority of these investigations emphasize patterns of  $\alpha$ -diversity, while comprehensive studies on  $\beta$ -diversity and its environmental drivers remain limited. Although the biodiversity of large benthic invertebrates in Chinese bays has been investigated (Yu et al., 2015), studies addressing the distribution of gastropods, the decomposition of their  $\beta$ -diversity, and the underlying environmental mechanisms shaping these patterns is still scarce.

$\beta$ -diversity quantifies the differences in species composition between distinct communities or ecosystems. In contrast to  $\alpha$ -diversity, which describes species richness and evenness within a single quadrat,  $\beta$ -diversity measures the rate of changes in species composition across spatial or environmental gradients at a regional scale, thereby reflecting ecological patterns and biogeographical characteristics.  $\beta$ -diversity can be measured using various metrics, among which the Bray-Curtis dissimilarity index is widely used, as it accounts for both species presence/absence and abundance (Anderson et al., 2011). To interpret the underlying mechanisms of community variation,  $\beta$ -diversity can be partitioned into two components: turnover (the complete replacement of species between sites) and nestedness (where species-poor communities form subsets of species-rich communities) (Gu et al., 2023). Analyzing these components is essential for understanding the spatial structure of mangrove gastropod communities across bay gradients, as it allows us to distinguish whether observed compositional changes are driven primarily by environmental filtering and habitat heterogeneity (turnover) or by non-random species loss due to disturbance or stress (nestedness) (Du et al., 2021; Gu et al., 2023).

In this study, we examined three mangroves in the semi-enclosed bays along the southeastern coast of China. Within each mangrove, we sampled three regions—the inner, mid, and outer regions—to analyze gastropod community composition and diversity patterns. Specifically, we addressed the following questions: (1) What are the spatial patterns of gastropod diversity within and among mangroves? (2) Which species contribute most to community differences among regions and mangroves? (3) Which environmental variables significantly

influence gastropod community composition, and do these driving factors vary among mangroves? This study provides empirical evidence to support the ecological conservation and sustainable management of benthic biodiversity in semi-enclosed coastal mangrove systems and offers a regional case study contributing to the scientific and policy objectives of the United Nations Decade of Ocean Science for Sustainable Development.

## 2 MATERIAL AND METHOD

### 2.1 Study site

We selected mature mangrove areas ( $\geq 15$  years old) in Dongzhaigang (DZG, Hainan), Yingluo Bay (ZJ, Zhanjiang), and Quanzhou Bay (QZ, Fujian) as study areas across southeastern China. These three sites have distinct tidal regimes, which are key drivers of environmental variability within mangrove ecosystems. Dongzhaigang is characterized by an irregular semidiurnal tide with a relatively gentle tidal dynamic and a smaller average range of approximately 1.0 m (Wang et al., 2025). Zhanjiang Yingluo Bay exhibits a more complex mixed tidal pattern, with an average tidal range of 2.53 m and a maximum range of up to 6.25 m, making it one of the largest tidal ranges along the Guangdong coast (Zhu et al., 2016). Quanzhou Bay experiences a regular semidiurnal tide with an average tidal range of about 4.5 m, reflecting a high-energy tidal environment (Ye et al., 2016). Mangrove forests within bays exhibit pronounced environmental gradients from the inner to the outer regions, resulting in distinct variations in species composition across zones. To investigate these patterns, each bay was divided into three survey sites: inner bay (IN), mid-bay (MID), and outer bay (OUT) (Fig.1). The geographic coordinates of each survey site are provided in Supplementary Table S1.

### 2.2 Research design and field investigation

Sampling was conducted at three study areas during the summer and autumn of 2024 (July–October). At the three sites (IN, MID, OUT) of each bay area, one tidal creek channel was selected, and surveys at adjacent mangroves were conducted along the creek. One 10-m $\times$ 10-m quadrat was established every 100 m, with five quadrats sampled per sites as replicates. To estimate biomass density and biomass per unit region, arboreal and benthic gastropods were sampled separately from three randomly placed 1-m $\times$ 1-m quadrats within

each large quadrat. For arboreal gastropods, all individuals were collected from the trunks and branches of mangroves located within the vertical projection of the quadrat. When a quadrat did not contain a substantial trunk, the nearest tree (within 1 m) overhanging the quadrat was sampled to approximate a 1-m<sup>2</sup> bark area. During gastropod sampling, vegetation surveys were also conducted within each large quadrat, recording tree species, diameter at breast height (DBH), and tree height to calculate aboveground biomass (Li et al., 2022a; Guangdong Provincial Administration for Market Regulation, 2024) and the Shannon-Wiener index of vegetation. Surface sediments (top 0–5 cm) from the large quadrats were collected and transported to the laboratory for analysis of physicochemical properties, including salinity, pH, clay content (clay%), sediment organic carbon (SOC), and total nitrogen (TN%) (Zhang et al., 2022). Seawater temperature, salinity, pH, and dissolved oxygen were measured in the tidal channels nearby using WTW Multi 3510 IDS water quality analyzer. Gastropod specimens were transported to the laboratory for species identification based on morphological characteristics (e.g., shell shape, size and features of aperture, sculpture and collumella). Identifications were verified with reference to the GBIF (Global Biodiversity Information Facility, <https://www.gbif.org/>) and WoRMS (World Register of Marine Species, <https://www.marinespecies.org/>) databases.

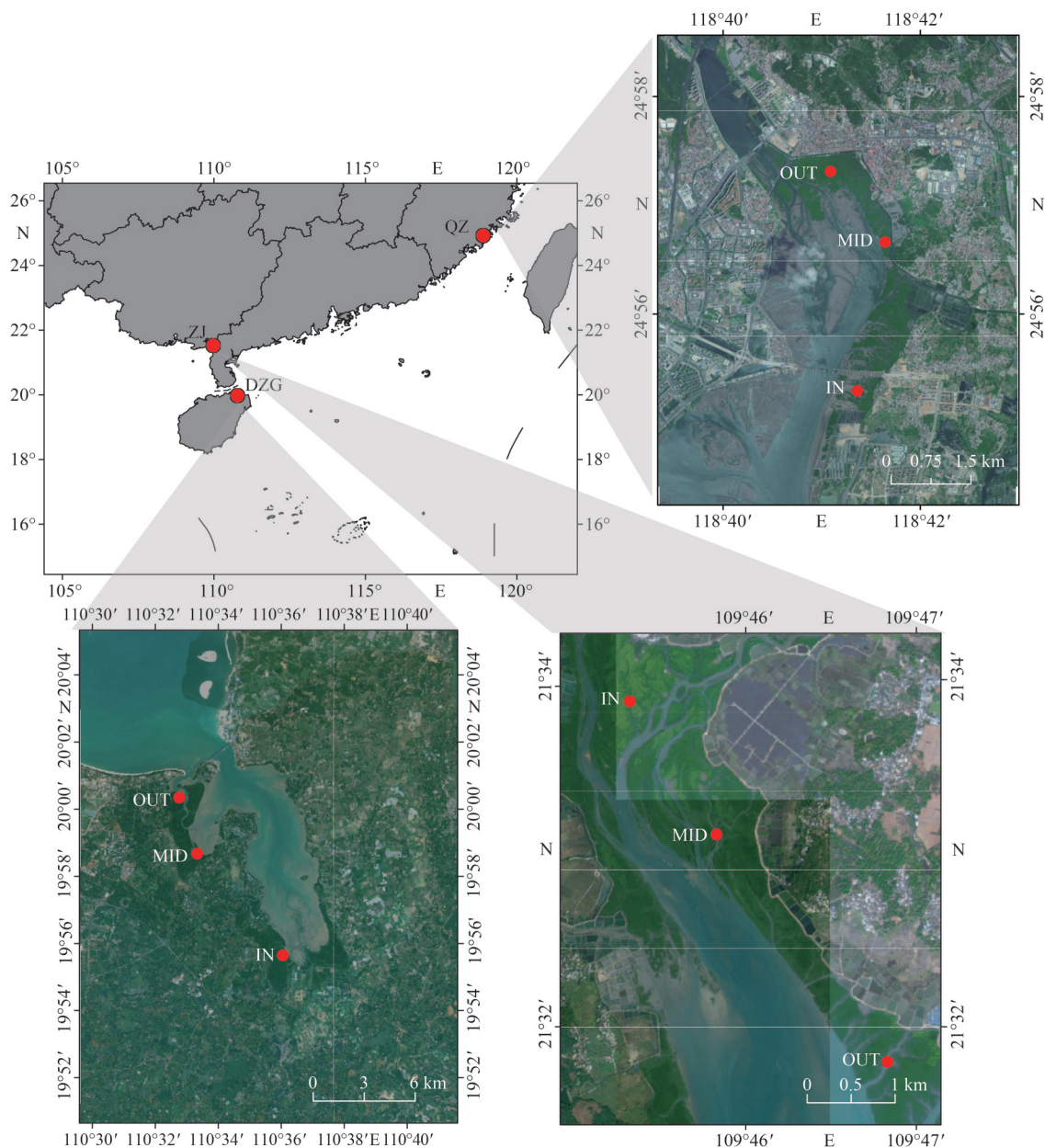
### 2.3 Data analysis

#### 2.3.1 Abundance and alpha ( $\alpha$ ) diversity calculations

All gastropod species collected within each 10-m $\times$ 10-m large quadrat were pooled and treated as a single sampling unit for analysis. Gastropod abundance (inds./m<sup>2</sup>) and biomass (g/m<sup>2</sup>) were calculated and compared across sites within each bay. Multivariate homogeneity of variance was tested using PERMDISP with the *betadisper* function in the R package *vegan*. Subsequently, PERMANOVA was conducted with the *adonis2* function to assess differences in gastropod community composition among bay locations (DZG, ZJ, QZ). Three  $\alpha$ -diversity indices, Shannon-Wiener, Simpson, and Pielou's evenness, were calculated using the diversity function in the R package *vegan*. Differences in  $\alpha$ -diversity indices among regions within each site were tested using the Wilcoxon rank-sum test.

#### 2.3.2 Beta ( $\beta$ ) diversity analysis

Prior to analysis, abundance data were log-



**Fig.1** Location of the study areas in Dongzhaigang (DZG, Hainan), Yingluo Bay (ZJ, Zhanjiang), and Quanzhou Bay (QZ, Fujian) of China

The sampling regions in each bay are marked as IN, MID, and OUT from the inner to the outer sites.

transformed using  $\lg(x+1)$ . Non-metric multidimensional scaling (NMDS) based on the Bray-Curtis dissimilarity matrix was employed to visualize variations in mangrove gastropod community composition (Zhang et al., 2022). The analysis was performed using the *vegan* package in R.

To identify taxa contributing to community differences across tidal flats, similarity percentage analysis (SIMPER) was applied to quantify the contribution of each species to average Bray-Curtis dissimilarity. Species contributing cumulatively to

the top 70% of community dissimilarity with  $P < 0.05$  were selected, and their abundances were visualized using stacked bar charts at the bay scale (Avaca et al., 2025). This process utilized the *Simper* function in the R package *vegan*.

In addition, the Sørensen index was used to calculate beta diversity for each intertidal zone, quantifying dissimilarity in gastropod community composition between paired samples. The *beta.div.comp* function in the R package *adespatial* was used to compute pairwise dissimilarities and partition

total beta diversity into turnover and nestedness components (Baselga and Orme, 2012; Avaca et al., 2025). Pairwise comparisons were conducted among sampling sites (IN, MID, OUT) within each bay (DZG, ZJ, QZ).

### 2.3.3 Environmental factor affecting community composition

Constrained distance-based redundancy analysis (dbRDA) was used to investigate the environmental determinants of community species composition. Environmental factors included: seawater temperature, salinity, pH, dissolved oxygen; sediment salinity, pH, sediment organic carbon (SOC), total nitrogen (TN), clay content; aboveground biomass and vegetation Shannon-Wiener index. Bray-Curtis distances were calculated using the *vegdist* function in the R package *vegan*. We then calculated the variance inflation factor (VIF) to check for multicollinearity among the constraint variables and removed any terms with a VIF value greater than 10 (Supplementary Table S2) (O'Brien, 2007). The significance of the constraint variables was tested using *anova* (*dbRDA\_result1*, *by=margin*) to evaluate their marginal effects of the explanatory variables. The direction and magnitude of the relationship between environmental variables and community composition were visualized using the dbRDA bivariate plot. All analyses were performed using R version 4.4.0.

## 3 RESULT

### 3.1 Abundance and alpha diversity of gastropods

A total of 27 gastropod species were recorded across the three bays, with 24 species in DZG, 15 species in ZJ, and 7 species in QZ (Supplementary Table S3). The most commonly encountered family was Littorinidae, which included four species within the genus *Littoraria*: *L. melanostoma*, *L. pallescens*, *L. ardouiniana*, and *L. sinensis*, along with one species from the genus *Mainwaringia*. The family Assimineidae was represented by two genera: *Optedicerus* (*O. breviculum*) and *Pseudomphala* (*P. latericea*). The most diverse genus was *Cerithidea* (including *C. cingulata*, *C. microptera*, *C. djadjariensis*, *C. tonkiniana*, *C. sinensis*), along with related genera such as *Cerithideopsis* (*C. largillierti*) and *Terebralia* (*T. sulcata*), all under the family Potamididae. Other families recorded include Stenothyridae (genus *Stenothyra*), Irvadiidae (genus *Irvadia*), Nassariidae (genus *Nassarius*), Batillariidae

(genus *Batillaria*), Neritidae (genera *Nerita*, *Neritina*, and *Clithon*), Ellobiidae (genera *Ellobium*, *Cassidula*, *Allochroa*, and *Pythia*), and Onchidiidae (genus *Onchidium*).

To assess the heterogeneity of gastropod communities among sites (IN, MID, OUT) within each bay (DZG, ZJ, QZ), homogeneity of dispersion tests were performed based on both abundance and biomass (Table 1). The results showed no significant differences in dispersion among the three bays (all  $P > 0.05$ ), indicating that the assumption of homogeneous variance was satisfied. Subsequently, PERMANOVA analyses based on Bray-Curtis distances revealed highly significant differences in gastropod community structures among the three bays for both abundance and biomass ( $P < 0.05$ ).

Boxplots of  $\alpha$ -diversity indices (Shannon-Wiener, Simpson, and Pielou's evenness) across sites and sampling locations showed a consistent spatial pattern: diversity was generally lowest at the inner bay (IN) and highest at the outer bay (OUT) (Fig.2). This trend was particularly pronounced in the higher-latitude bays ZJ and QZ, where  $\alpha$ -diversity indices at OUT were significantly greater than those at IN sites (Wilcoxon test,  $P < 0.05$ ).

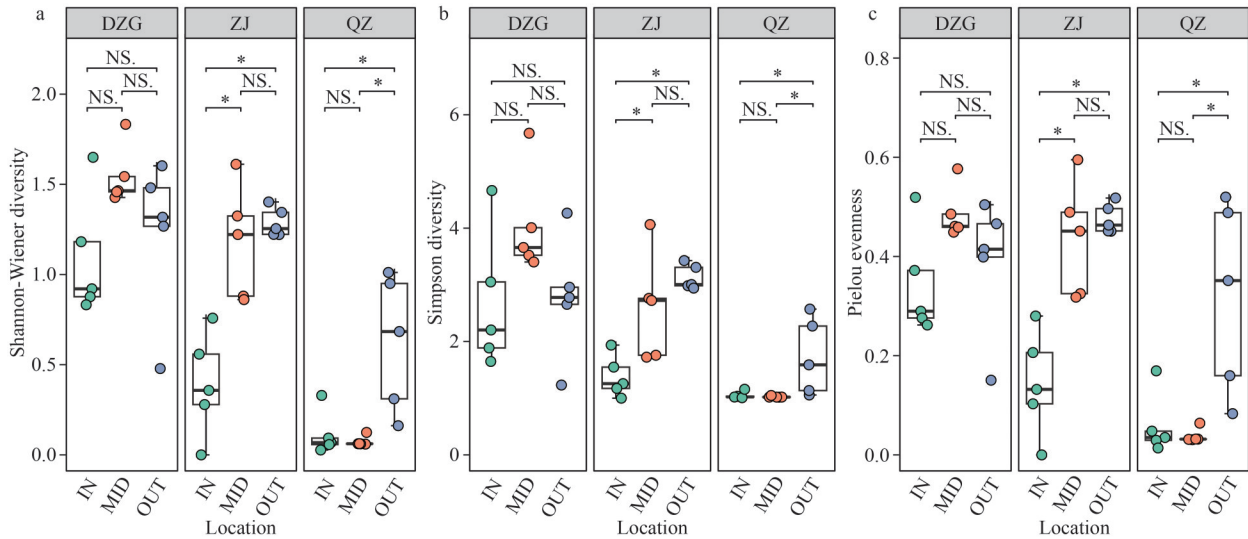
### 3.2 Beta diversity comparison of gastropods

SIMPER analysis (Fig.3a; Supplementary Table S4) revealed significant differences in dominant community composition among sites, suggesting that region variation at the bay was mainly driven by species replacement in DZG. For instance, *Stenothyra hokkaidonis* and *Neritina violacea* occurred exclusively at the inner bay, where the family Littorinidae was absent. In middle bay *Optedicerus breviculum* was absent, while Littorinidae was more

**Table 1 PERMDISP and PERMANOVA test results for abundance and biomass in the three bays, respectively**

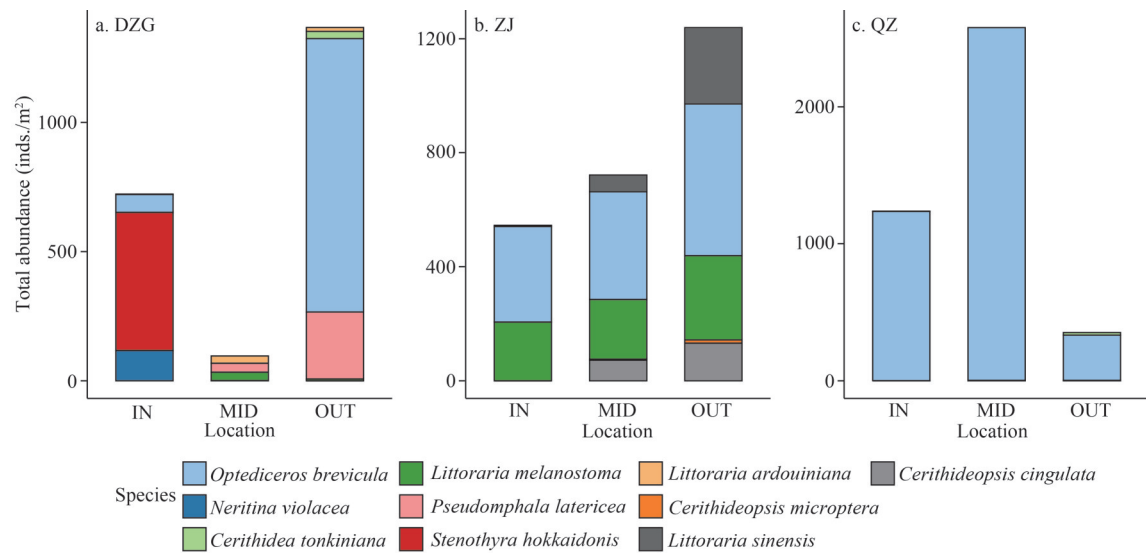
| Area | Metric    | PERMDISP<br><i>P</i> -value | PERMANOVA<br><i>R</i> <sup>2</sup> | PERMANOVA<br><i>P</i> -value |
|------|-----------|-----------------------------|------------------------------------|------------------------------|
| DZG  | Abundance | 0.105                       | 0.563                              | 0.001***                     |
| DZG  | Biomass   | 0.268                       | 0.613                              | 0.001***                     |
| ZJ   | Abundance | 0.395                       | 0.312                              | 0.034*                       |
| ZJ   | Biomass   | 0.162                       | 0.275                              | 0.026*                       |
| QZ   | Abundance | 0.103                       | 0.489                              | 0.003**                      |
| QZ   | Biomass   | 0.622                       | 0.496                              | 0.003**                      |

\*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ .



**Fig.2 Comparison of gastropod alpha diversity indices across the three bay regions (inner bay, IN; mid-bay, MID; outer bay, OUT)**

a. Shannon-Wiener diversity index; b. Simpson diversity index; c. Pielou's evenness index. Colors represent the three regions: green (IN), orange (MID), and purple (OUT). NS: not significant; \*:  $P < 0.05$  (Wilcoxon test).



**Fig.3 Abundance of species contributing to community differences of gastropod in the three bays**

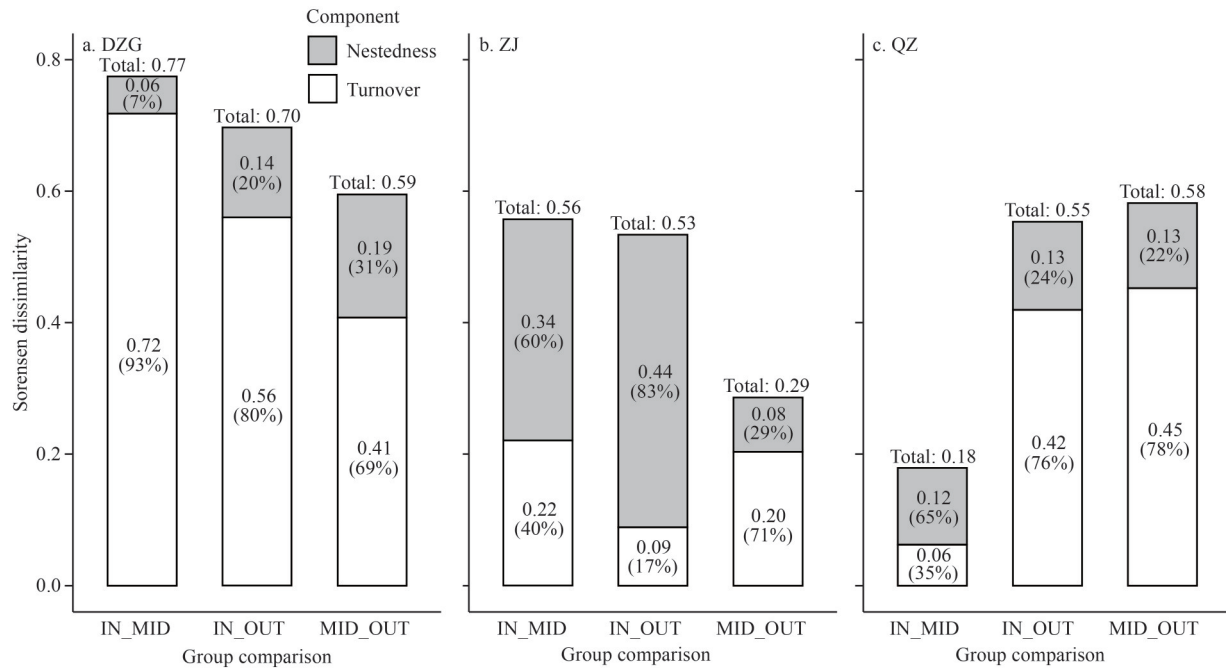
The y-axis limits vary among panels to best visualize site-specific abundance ranges.

abundant compared to other bay regions. Notably, the relative dominance of *Optedicerus breviculum* increased markedly at the outer bay. This pattern likely reflects a distinct spatial environmental gradient or ecological niche differentiation among species.

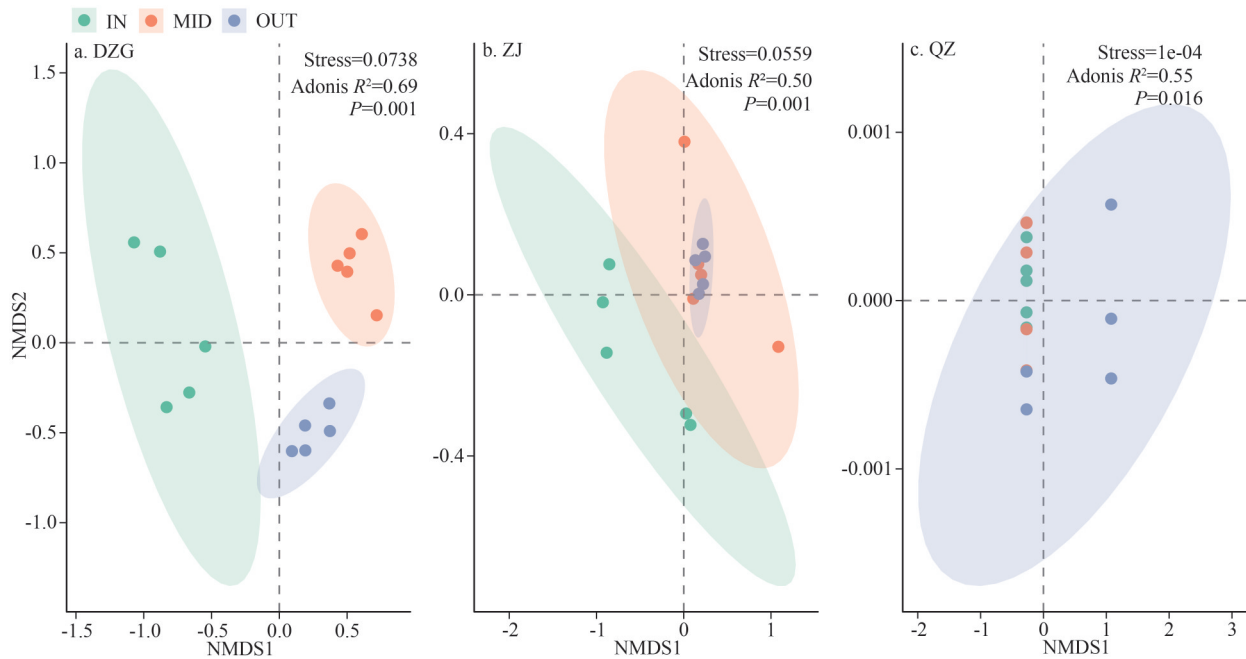
Within the internal sampling sites of different bays, the DZG bay mouth exhibited the highest total  $\beta$ -diversity (IN vs. MID=0.77), with species turnover as the dominant component (Fig.4a). In contrast, the community structure at the ZJ bay mouth was dominated by nestedness (Fig.4b), largely due to the

disappearance of the species *C. cingulata* in the inner bay (Fig.3b), and potentially influenced by strong environmental filtering. The QZ bay mouth community exhibited low heterogeneity (total  $\beta < 0.6$ ), yet species turnover remained the dominant mechanism, mainly reflected in the occurrence of *C. tonkiniana* (Fig.4c).

As shown by the NMDS results (Fig.5), in DZG (Fig.5a), the low stress (0.073  $8 < 0.1$ ) indicating excellent ordination fit, the high  $R^2$  (0.69) means the grouping variable (IN, MID, OUT) explains 69% of the variation in community structure, and significant



**Fig.4 Spatial beta diversity between sampling points of gastropod in the three bays**



**Fig.5 Non-metric multidimensional scaling (NMDS) ordination of the mangrove gastropods communities for each study site**

a. Dongzhaigang (DZG); b. Zhanjiang Yingluo Bay (ZJ); c. Quanzhou Bay (QZ). Within each ordination, ellipses (e.g., 0.95 confidence) encompass samples from the inner (IN), middle (MID), and outer (OUT) regions of the respective bay.

$P$ -value (0.001) together demonstrate highly distinct and statistically robust community differences among its groups. Likewise, in ZJ (Fig.5b), the exceptionally low stress (0.055 9), substantial  $R^2$  (0.50), and high significance ( $P=0.001$ ) likewise support strong and valid group separation. In QZ

(Fig.5c), the extremely low stress value (1e-04) likely reflects high homogeneity in community composition across sites, indicating low beta-diversity within the area. Despite this uniformity, the moderate  $R^2$  (0.55) and significant  $P$ -value (0.016) still confirm statistically well-defined differentiation

among the groups.

Although significant bay-scale differences in community composition were detected among the three regions (adonis,  $P < 0.05$ ), in ZJ and QZ, differentiation among inner bay, middle bay, and outer bay communities was not evident in two-dimensional space. This was mainly due to abundance variations of the same species across bay locations in ZJ and QZ. In particular, the dominance of the *O. breviculum* masked bay-scale differences, making it difficult to distinguish communities (Fig. 3b & c). In contrast, distinct species compositions among different bay locations at the DZG site resulted in clearer community differentiation, which was more effectively captured by NMDS.

### 3.3 Environmental factor affecting community composition

At the DZG bay, the dbRDA model explained 45.3% of the variation in community composition (Fig. 6a, dbRDA1: 26.71%; dbRDA2: 18.06%). The ordination revealed a two-level separation among sites. First, IN samples were clearly separated from both MID and OUT samples along dbRDA1, a gradient primarily associated with aboveground biomass and water pH. Second, within the MID and OUT cluster on the right side of the plot, OUT samples were positioned in the upper right quadrant, opposing MID samples in the lower right along dbRDA2; this separation correlated with gradients in soil salinity and clay content. Among these variables, salinity and aboveground biomass showed trends toward significance ( $P < 0.1$ ). This structured separation suggests that distinct environmental

filters operate at different spatial scales: broad bay-scale gradients (aboveground biomass/water pH) separate the inner bay community, while more localized factors (sediment texture) further differentiate the middle and outer bay assemblages, contributing to the species turnover observed at DZG.

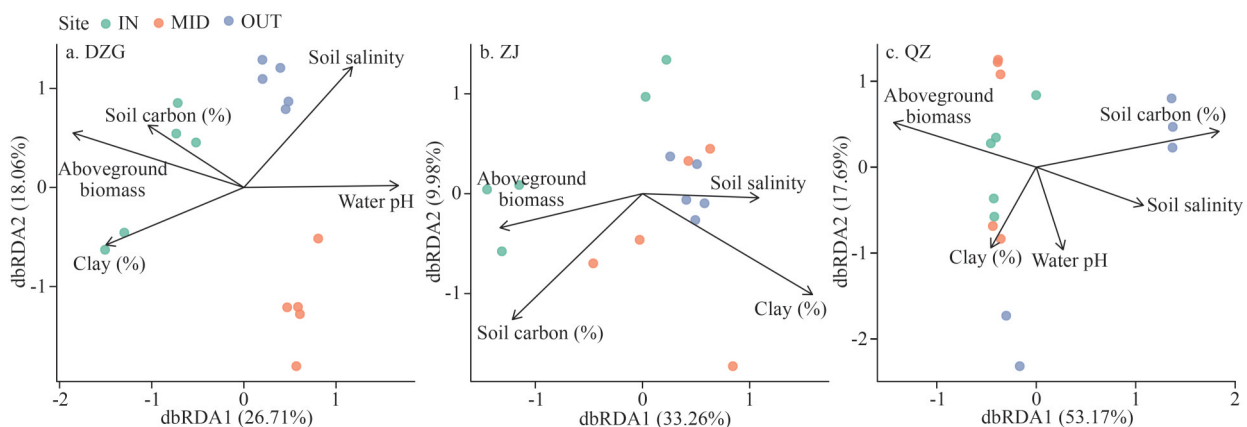
At ZJ Bay, the dbRDA model explained 43.1% of community variation (dbRDA1: 33.26%; dbRDA2: 9.89%). The ordination showed a partial separation of sites: while the IN group was distinct, the MID and OUT groups exhibited considerable overlap (Fig. 6). Permutation tests indicated that clay content was the only statistically significant driver ( $P < 0.05$ ). Soil organic carbon (SOC) exhibited a marginal, non-significant influence ( $P = 0.057$ ), suggesting it may contribute to the observed pattern alongside other factors but is not a primary determinant.

At the QZ Bay mouth, the dbRDA model explained 70.9% of the community variation (dbRDA1: 53.17%; dbRDA2: 17.69%). SOC was the only significant explanatory variable ( $P < 0.05$ ). Variation in community composition at QZ Bay may therefore be primarily driven by differences in sediment organic matter.

## 4 DISCUSSION

### 4.1 Spatial pattern of gastropods in the mangrove

Our results showed that  $\alpha$ -diversity and evenness were generally higher at the outer bay and lower in the inner bay. Similar spatial patterns have been reported for other large benthic organisms in different bays (Du et al., 2008; Barros et al., 2014;



**Fig. 6 Distance-based redundancy analysis (dbRDA) showing the relationship between environmental factors and gastropod community composition across the three bays**

Results are presented separately for Dongzhaigang (DZG), Hainan (a); Yingluo Bay (ZJ), Guangdong (b); Quanzhou Bay (QZ), Fujian (c). Vectors represent environmental variables, and their length and direction indicate the strength and correlation of their influence on community structure.

Avaca et al., 2025). For example, the molluscan alpha diversity increased from impoverished inner sites to well-structured assemblages at outer sites in northern Patagonian tidal flats (Avaca et al., 2025). This appears to be a general phenomenon that is largely independent of latitude (Barros et al., 2014). A classic paradigm in estuarine ecology, the “Artemimum zone,” describes reduced species richness in the mid-salinity zone, producing a U-shaped distribution with higher diversity at both ends of the salinity gradient (Remane, 1934). However, this pattern has not been consistently observed in subtropical estuaries and mangrove systems (Alves et al., 2020; Zamprogno et al., 2023). Semi-enclosed mangrove-fringed bays are inherently complex, with species diversity influenced by multiple factors beyond salinity. This pattern likely also arises from greater habitat complexity in outer bay regions, where features like pneumatophores, woody debris and oyster reefs provide more ecological niches and refugia from predation and desiccation, supporting a wider array of gastropod species (Hookham et al., 2014). Additionally, stronger water exchange near the bay mouth enhances nutrient supply and reduces hypoxia (Ohgaki and Kosuge, 2005), supporting higher diversity compared to the inner bay. These mechanisms collectively contribute to the observed gradient of increasing alpha diversity from the inner to outer bay regions.

Many estuarine species in tropical and subtropical systems exhibit strong tolerance to moderate salinity fluctuations. In relatively undisturbed tropical estuaries, community succession along salinity gradients is commonly observed (Barros et al., 2012; Alves et al., 2020). Successional dominance reflects ecological processes driven by niche differentiation and environmental filtering, whereas nested dominance arises mainly from species loss and stress tolerance, often associated with human disturbance and environmental degradation (Barros et al., 2014). Severe human disturbance can increase the nested component of  $\beta$ -diversity, as human disturbance amplifies nested signals through environmental homogenization (Barros et al., 2014). Importantly, increases in nestedness may precede detectable declines in  $\alpha$ -diversity, making it an early-warning signal of ecosystem degradation. Among the three bays, ZJ exhibited the strongest environmental homogenization and the most pronounced nested community structure, suggesting that it has been most heavily affected

by human disturbance. This is consistent with the fact that aquaculture activities are particularly intensive around the mangroves of ZJ (Zhang and Chen, 2022), which likely alter gastropod distribution. Therefore,  $\beta$ -diversity partitioning is not merely a descriptive analytical step, but a mechanistic tool capable of distinguishing natural successional structuring from disturbance-driven species loss. This highlights its potential utility in estuarine ecosystem monitoring and conservation assessment.

#### 4.2 Species' unique adaptation to the bay environment

In this study, the family Littorinidae and the species *Optediceros breviculum* were present throughout the entire bay, although their abundances varied markedly among different regions. Littorinidae abundance was notably higher in ZJ than that in the other bays, and it was elevated across the inner bay, the middle bay, and the outer bay relative to corresponding regions in the other bays. Overall, Littorinidae maintained relatively high abundances throughout the bay. Littorinidae are herbivorous species, primarily feeding on mangrove derived detritus and phytoplankton (Chen et al., 2017; Wu et al., 2020). Their elevated abundance in ZJ may be linked to nutrient inputs from nearby aquaculture operations. Nutrient enrichment from aquaculture can enhance the growth of adjacent vegetation, thereby providing favorable food resources that support Littorinidae populations (Cabral-Oliveira et al., 2009). Similar to other arboreal *Cerithidea* species, *C. tonkiniana* is intolerant of prolonged flooding and climbs mangroves to avoid tidal waters (Reid, 2014), typically occupying higher-elevation areas to reduce locomotion energy costs. In the present study, this species was observed across all three sites of ZJ Bay, whereas in DZG and QZ it was restricted to the bay mouth. Field observations further indicated that the species predominantly inhabits mangrove trunks near the shoreline. Its absence from other sites in DZG and QZ may be related to local elevation gradients, which warrants verification using detailed topographic data. This distribution suggests that the availability of particular mangrove species suitable for climbing (e.g., with favorable trunk texture) may be a critical factor, as seen in the congeneric *C. decollata*, which selectively inhabits *Avicennia* marinatrunks in the Western Indian Ocean (Vannini et al., 2006).

While in this study, species identification in

this study was based on well-documented shell morphological characters, we recognize that morphological taxonomy alone can sometimes overlook cryptic species complexes, particularly within diverse genera. The use of molecular markers (e.g., mitochondrial COI barcoding) would provide an additional layer of verification for ambiguous specimens and could reveal hidden genetic diversity not apparent from morphology. Future research aiming to resolve fine-scale taxonomic boundaries or biogeographic patterns within these mangrove gastropod communities would be significantly strengthened by integrating molecular data with traditional morphological examination.

#### 4.3 The influence of environmental factors on the distribution of gastropods in bays

Our study revealed that gastropod community distributions across the three bays were closely associated with multiple environmental factors, with salinity, sediment organic carbon content, sediment clay content, and aboveground biomass exerting particularly significant influences.

Salinity emerged as a critical determinant of gastropod distribution. Its influence operates both through direct physiological constraints and indirectly by modifying habitat structure. A previous study has demonstrated that salinity modulates gastropod metabolism, reproduction, and larval development via osmoregulatory mechanisms (Maia and Coutinho, 2016). As demonstrated by Van Diggelen and Montagna (Van Diggelen and Montagna, 2016), salinity variance can be a stronger predictor of macrofaunal diversity than mean salinity, acting as a persistent environmental disturbance that filters out less tolerant species. Its influence operates both through direct physiological constraints and indirectly by modifying habitat structure. In DZG Bay, low salinity conditions coupled with elevated aboveground biomass contributed to marked community differentiation, predominantly driven by species turnover, indicating that relatively stable high-salinity zones may facilitate the establishment of particular species. Furthermore, salinity is a primary driver of mangrove species zonation, influencing their distribution along estuarine gradients. This is exemplified by the dominance of salt-tolerant species like *Avicennia marina* in high-salinity areas (Zhang et al., 2001). The differential salt tolerance among mangrove species is underpinned by distinct physiological adaptations, such as the compartmentalization of salts and the accretion of condensed tannins in non-secretor species (Wang

and Lin, 2003; Zhu et al., 2023). Differences in mangrove species, in turn, create distinct microhabitats (e.g., through variations in root architecture and bark texture), which directly affect the availability of suitable attachment substrates for gastropods (Skilleter and Warren, 2000). Future climate change is projected to increase precipitation variability, which is strongly linked to fluctuations in estuarine salinity at the bay scale (Wachnicka et al., 2013; Thirumalai et al., 2018). Given that such heightened salinity variability is anticipated, gastropod populations may experience intensified environmental stress, potentially leading to shifts in their distribution patterns.

In addition to salinity, the interactive effects of hydrodynamics and tidal elevation form a fundamental physical template shaping gastropod  $\alpha$ - and  $\beta$ -diversity along the inner-to-outer bay gradient. Tidal elevation, governing inundation frequency, acts as a primary environmental filter, often showing greater influence on macrobenthic community structure than vegetation types (Chen et al., 2009). Our subtropical system showed lower diversity at inner-bay (functionally higher-elevation) sites, but contrasting patterns were observed in a temperate tidal flat that macrozoobenthic biomass decreased but species richness and diversity increased towards higher elevations (Dewenter et al., 2023). This discrepancy highlights that the expression of the elevational gradient might be modulated by the regional climatic context. Sediment physicochemical properties also play a key role in structuring gastropod communities. The proportions of clay particles and sedimentary organic carbon are closely associated with gastropod distribution. In ZJ Bay, sediment organic carbon content and clay fraction emerged as primary drivers of community nestedness patterns. Organic-rich clay sediments can enhance resource availability and water retention (Passy, 2010; Faseyi et al., 2022), thereby supporting higher community diversity. Conversely, sediments with high clay content may adsorb pollutants (e.g., polynuclear aromatic hydrocarbons) (Zhang et al., 2004), potentially threatening gastropod health via trophic transfer. Additionally, dynamic processes in the sedimentary environment, such as excessive sedimentation rates leading to habitat burial or erosion processes disrupting stability, may limit gastropod settlement and reproduction (Salamon et al., 2024).

Mature mangrove stands, with their complex root systems and abundant litter layers, offer shelter, food, and diverse ecological niches for gastropods

(Nagelkerken et al., 2008). The influence of aboveground biomass on gastropod communities varied across bays. In DZG, lower aboveground biomass (likely reflecting simpler stand structure) combined with high salinity explained the observed community differences. In ZJ and QZ, although aboveground biomass was not statistically significant, its vector orientation suggested a potential, yet subordinate, influence on composition. Overall, sediment organic carbon and salinity gradients emerged as more direct and consistent drivers of community structure across the study sites, while the role of structural complexity (as indicated by aboveground biomass) appeared context-dependent. These findings indicate a potential association between mangrove stand structural attributes and gastropod distribution.

Notably, environmental factors often interact, producing compound effects. For instance, high clay content may exacerbate sediment hypoxia under low-salinity conditions, whereas under high-salinity conditions it can enhance water retention, resulting in context-dependent effects (Herlemann et al., 2011). Furthermore, interactions between temperature and salinity may modify gastropod tolerance thresholds (Lillebjerka et al., 2023). This regional specificity, observed in our study, underscores that environmental effects on gastropods are scale-dependent and not universally consistent. For instance, while water temperature, salinity, and organic carbon significantly shaped communities in our system, other studies in different contexts have found factors such as turbidity, dissolved oxygen, or anthropogenic activities to be more influential (Samsi et al., 2018). This highlights the necessity of contextualizing findings within specific local environmental settings and cautioning against overgeneralization across disparate mangrove ecosystems.

#### 4.4 Implication for mangrove conservation and management

The spatial patterns and assembly mechanisms of gastropod communities revealed in this study provide a scientific basis for spatially explicit conservation strategies in mangrove-fringed bays. The consistent increase in  $\alpha$ -diversity from inner to outer bay zones, coupled with the contrasting  $\beta$ -diversity mechanisms (species turnover in Dongzhaigang and Quanzhou Bay versus nestedness in Zhanjiang Bay), highlights the need for a differentiated management framework.

This framework should prioritize the protection

of outer bay zones as core biodiversity areas, given their high species richness and stable environmental conditions. Conservation efforts here must focus on maintaining natural hydrological and sedimentary processes. In contrast, the inner bay of Zhanjiang Bay, where nestedness indicates significant anthropogenic disturbance and species loss, requires targeted ecological restoration. Management should aim to mitigate local stressors, particularly from aquaculture, to restore habitat integrity. For Dongzhaigang and Quanzhou Bay, where species turnover reflects an intact environmental gradient, the primary goal is to preserve the full ecological continuum from the inner to outer bay, ensuring the maintenance of regional species pools.

Therefore, effective mangrove conservation should adopt a spatially adaptive approach. This involves protecting outer-bay biodiversity hotspots, restoring degraded inner-bay habitats, and safeguarding the natural connectivity and environmental gradients across the entire bay system. Integrating  $\alpha$ - and  $\beta$ -diversity metrics into monitoring can thus directly inform coastal restoration planning and blue carbon ecosystem management, supporting both national conservation goals and international sustainability initiatives.

## 5 CONCLUSION

This study elucidates how natural gradients and human pressures jointly shape gastropod biodiversity in mangrove-fringed bays along southeastern coast of China. The consistent increase in  $\alpha$ -diversity from inner to outer bay zones, along with the contrasting  $\beta$ -diversity mechanisms (species turnover vs. nestedness) across different bays, underscores that biodiversity patterns are governed by distinct assembly processes in response to local environmental and anthropogenic contexts. These findings advance our understanding of mangrove benthic ecology by highlighting that  $\beta$ -diversity decomposition, particularly the turnover to nestedness ratio, serves as a sensitive indicator for distinguishing niche-based community structuring from disturbance-driven species loss.

The spatial and mechanistic insights offer direct implications for mangrove conservation and restoration. First, the outer bay zones, supporting the highest diversity and stable communities, should be prioritized as core protection areas to preserve biodiversity hotspots. Second, the strong nestedness signal detected in Zhanjiang Bay calls for targeted restoration in its inner reaches, where reducing anthropogenic pressures (e.g., aquaculture expansion)

is essential to reverse species loss. Finally, the turnover dominated gradients in Dongzhaigang and Quanzhou Bay emphasize the need to maintain natural hydrological connectivity and environmental heterogeneity across the entire estuarine.

Integrating  $\alpha$  and  $\beta$  diversity metrics into routine monitoring can strengthen ecological assessments and support spatially explicit management. Future studies should integrate biodiversity surveys with direct measurements of anthropogenic stressors. Such an approach will enhance the capacity to design effective conservation strategies, contributing to both national mangrove protection goals and the global objectives of the UN Decade of Ocean Science for Sustainable Development.

## 6 DATA AVAILABILITY STATEMENT

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## 7 ACKNOWLEDGMENT

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### Electronic supplementary material

Supplementary material (Supplementary Tables S1–S4) is available in the online version of this article at <https://doi.org/10.1007/s00343-026-5491-z>.