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Integrating eDNA metabarcoding and functional trait analysis to uncover fish community structure and assembly mechanism in the Taiwan strait

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Marine fish communities in coastal systems are increasingly shaped by environmental gradients associated with anthropogenic pressures and climate variability, yet how these factors influence community assembly and functional traits remain poorly understood. In this study, environmental DNA (eDNA) metabarcoding using the 12S MiFish primer with 33 water samples was integrated with taxonomic and functional diversity analyses, co-occurrence network analysis, the neutral community model, hierarchical modeling of species communities, and single-trait-based community-weighted means to investigate fish communities in the Taiwan Strait (TWS). This interdisciplinary approach provides both a unique perspective and a comprehensive framework for fish biodiversity assessment. Fish communities exhibited high modularity and weak interspecific interactions, with an uneven distribution of species within functional space, indicating elevated ecological vulnerability. Community assembly was jointly governed by stochastic and deterministic processes, with NO_2^- identified as a significant environmental driver shaping fish community assembly. Notably, fish communities in the inshore and principal axis regions exhibited higher clustering coefficient but lower network modularity compared to other regions. Hierarchical modeling of species communities and community-weighted means further indicated clear distributional and trait differences among fish from the estuarine to offshore areas, consistent with species-specific responses to environmental gradients from inshore to offshore areas. Overall, TWS fish communities are dominated by species with very small and small body-length traits, while reef-associated fishes are mainly concentrated in inshore and midshore regions. Fish community assembly and functional traits in TWS exhibited systematic variation along the offshore distance gradient and were jointly modulated by key environmental factors.

KEYWORDS

community stability, deterministic processes, eDNA metabarcoding, stochastic processes, Taiwan strait

1 Introduction

Marine ecosystems are experiencing unprecedented pressures from anthropogenic activities and climate change, which have profoundly altered community dynamics (Thomsen et al., 2012). As an essential component of marine ecosystems, fish communities play a critical role in maintaining ecological balance and sustaining fisheries resources (Pinna et al., 2023). The Taiwan Strait (TWS) is strongly influenced by riverine inputs, fishing activities, and maritime navigation; however, our understanding of how fish communities in this region respond to environmental gradients remains limited.

Conventional approaches to monitoring anthropogenic impacts on marine ecosystems face significant limitations, as traditional techniques often fail to provide a complete picture of biodiversity change. Methods such as bottom trawling are not only invasive and labor-intensive but also exhibit low sensitivity for detecting rare or elusive species. Owing to these inefficiencies, such approaches offer limited capacity for capturing rapid shifts in fish community structure over short timescales (Keck et al., 2022; Ruan et al., 2022). These constraints highlight an urgent demand for more efficient and non-invasive biomonitoring tools. In this context, environmental DNA (eDNA) metabarcoding has emerged as a powerful high-throughput approach. eDNA comprises genetic material shed by organisms into their surroundings—such as water or sediments—via skin cells, excretions, mucus, gametes, or decomposing remains (Stat et al., 2017; West et al., 2024; Westgaard et al., 2024). By enabling simultaneous identification of multiple taxa through parallel sequencing, eDNA metabarcoding has become an increasingly common tool in large-scale marine biodiversity surveys (Fujii et al., 2019; Gold et al., 2021; He et al., 2023b; Stat et al., 2017). Recent studies have underscored the rapid development and applicability of this technique, confirming its utility for monitoring marine biodiversity, particularly fish assemblages (Beridze et al., 2023; Fonseca et al., 2023). However, current eDNA-based research has largely centered on documenting species presence, including inventories of biodiversity, invasive species, rare taxa, and threatened populations (Beridze et al., 2023; Fonseca et al., 2023). Although numerous studies have used eDNA to analyze fish communities, traditional biodiversity assessments still focus primarily on taxonomic diversity (Fonseca et al., 2023; He et al., 2023a). In recent years, eDNA-based research has gradually begun to incorporate functional traits. Compared with taxonomic diversity, functional diversity is a more direct indicator of ecosystem functioning, as it reveals the roles of communities in ecosystem processes and their responses to environmental drivers (Cantera et al., 2025). However, studies that systematically examine how species functional traits influence community stability remain relatively limited (McKinley et al., 2023).

Functional diversity refers to the variety of ecological functions carried out by organisms in an ecosystem. In marine environments, functional diversity assessments have been widely employed across various habitats and taxonomic groups, aiding in the understanding of species' functional distributions and the dynamics of ecological processes. Such analyses provide critical information on ecosystem

structure and functioning (McKinley et al., 2023; Mouillot et al., 2014). Functional traits—reflecting ecological differences among species—are directly linked to the morphological, physiological, reproductive, or behavioral attributes associated with organisms' ecological roles (Gomes et al., 2023). How these traits respond to disturbances, and the degree of trait variation among co-occurring species, shape the overall resilience of ecosystems to environmental changes (Lamothe et al., 2018; Rincon-Díaz et al., 2021). The loss of biodiversity represents a major threat to ecosystem processes and associated services (Bellwood et al., 2012). Functional redundancy—when multiple species perform similar ecological roles—can help buffer ecosystem functions against species declines by enabling redundant taxa to occupy comparable niches, thereby supporting ecosystem recovery following perturbations (Mouillot et al., 2014; Rocha et al., 2023). Nevertheless, even in highly diverse systems such as coral reefs, functional redundancy may be inadequate to compensate for species loss. Many vital ecological functions are often sustained by a narrow set of species within limited functional groups, increasing ecosystem susceptibility to biodiversity reduction (Mouillot et al., 2014).

Community structure arises from the complex interaction between stochastic and deterministic processes. Niche theory and neutral theory provide complementary conceptual frameworks for understanding these respective mechanisms in community assembly (Hubbell, 2001; Li et al., 2024). Niche theory emphasizes the role of deterministic factors—such as abiotic conditions (e.g., pH, temperature, dissolved oxygen) and biotic interactions (e.g., competition, predation, mutualism)—in shaping species composition (Montanyès et al., 2023; Shi et al., 2023). In contrast, neutral theory attributes community structure primarily to stochastic events including birth, death, dispersal limitation, speciation, and ecological drift, assuming functional equivalence among species (Janzen et al., 2017; Liang et al., 2024; Woodcock et al., 2007). Although these perspectives are often presented as opposing views, growing evidence indicates that both deterministic and stochastic processes operate simultaneously in structuring ecological communities (Liao et al., 2016). A major challenge in ecology lies in quantifying the relative contributions of these processes to fish community assembly and elucidating the underlying species aggregation patterns (Liao et al., 2016). Empirical research has revealed considerable variability in assembly mechanisms across different aquatic ecosystems. Therefore, determining whether stochastic or deterministic factors dominate fish community organization, along with identifying key environmental drivers, is crucial for unraveling the mechanisms that govern community formation and maintenance (Li et al., 2024). Among the tools available for this purpose, the Neutral Community Model (NCM), introduced by Sloan et al., continues to be widely used for quantifying the influence of stochasticity on community assembly (Chen et al., 2019; Sloan et al., 2006).

Ecological stability encompasses multiple dimensions, and co-occurrence network analysis has become a principal method for predicting species interactions and community structure, thereby providing deeper insights into ecosystem stability (Gu et al., 2023; Zhang et al., 2022). This analytical approach is extensively applied to study species coexistence patterns and inferred interactions

across a wide range of habitats (Gad et al., 2020; Mo et al., 2021; Sun et al., 2024). Given that interspecific interactions are fundamental to sustaining species diversity and ecosystem functioning, co-occurrence network analysis offers a robust framework for assessing ecosystem stability (Guan et al., 2021).

The Taiwan Strait (TWS), located on the continental shelf of the China Seas, is a vital passage connecting the East China Sea and the South China Sea. It spans approximately 350 km in length and 180 km in width, with an average depth of 60 m (Zhang et al., 2009). This strait serves as an important migratory corridor for fish and is influenced by three distinct water masses: the cold, low-salinity Zhe-Min Coastal Current; the warm, high-salinity Kuroshio Current; and the South China Sea Warm Current, which exhibits intermediate temperature and salinity properties (Hu et al., 2010). Furthermore, the region is periodically affected by tropical storms and typhoons, which can trigger heavy rainfall, intense vertical mixing, and upwelling events (Ko et al., 2016). The Taiwan Strait supports rich fishery resources, functioning as a significant upwelling fishing ground on the southeastern continental shelf of China (Ju et al., 2022; Xing et al., 2018). As the relative influence of the three major currents varies seasonally, their dynamic interplay results in distinct chemical and hydrological conditions, which in turn are expected to influence fish community structure across different spatial scales (Hsiao et al., 2021; Xing et al., 2018). Understanding fish biodiversity and community structure in the TWS is therefore crucial for sustainable fishery management. However, previous studies relying on traditional survey methods have often been limited in taxonomic coverage, leading to a fragmented understanding of fish diversity and community distribution patterns in this region.

This study is the first to integrate eDNA metabarcoding, functional diversity analysis, species co-occurrence networks, single-trait-based community-weighted mean, the neutral community model and hierarchical modeling of species communities in the TWS, thereby establishing a comprehensive framework for characterizing the fish community. To achieve this, eDNA metabarcoding was employed in conjunction with taxonomic and functional diversity to comprehensively characterize fish biodiversity in the TWS. We hypothesized that the fish community in TWS would exhibit low stability due to the influence of anthropogenic disturbance. Additionally, this study aimed to evaluate the influence of offshore distance on both the community composition and functional traits. It was further hypothesized that offshore distance would be a key driver of variations in the taxonomic composition and associated shifts in the functional traits of the fish community.

2 Materials and methods

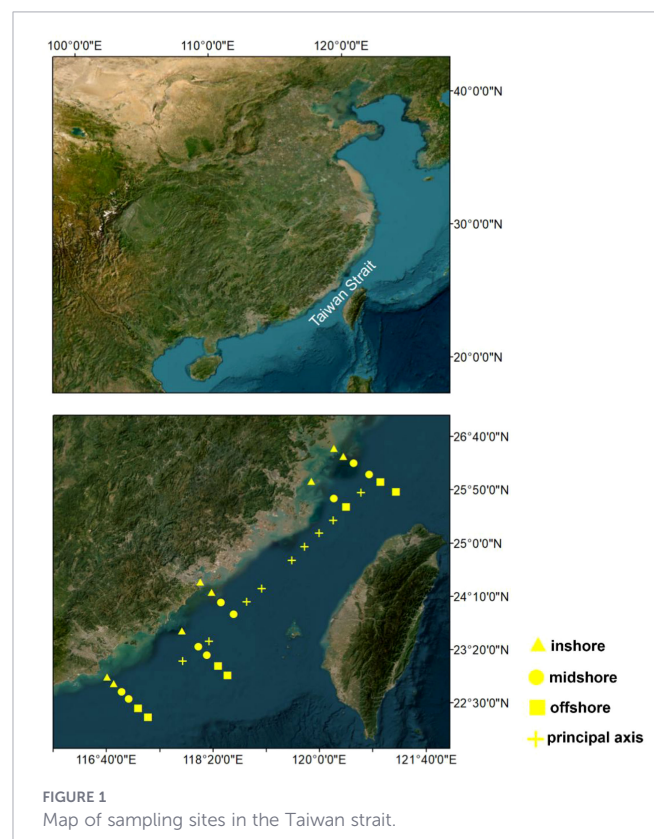
2.1 Field sampling and eDNA sampling

Seawater samples for eDNA analysis were collected during August in 2022 (Figure 1). The sampling sites were categorized into inshore, midshore, offshore, and principal axis areas based on offshore distance and regional hydrodynamic characteristics (Qin et al., 2023; Zhu et al.,

2025). The principal axis areas correspond to sites aligned with the dominant summer current in TWS, which is primarily associated with the northward intrusion of South China Sea Water (Jan et al., 2002; Wu et al., 2007). At each station, 1 L of seawater was collected and immediately filtered on-site using a 0.2 μm pore-size polycarbonate membrane filter (Millipore, USA). The filter membranes were then placed into 2 mL cryogenic tubes (Axygen, USA) and immediately stored at -80°C until DNA extraction. In addition, three field blanks were collected to serve as negative controls for contamination monitoring. Prior to filtration, all sampling equipment and filters were rinsed with Milli-Q water. For the analysis of environmental factors, 50 mL of pre-filtered seawater was collected at each station using centrifuge tubes. In the laboratory, AA3 Continuous Flow Analyzer (SEAL Analytical, Germany) was employed to determine the level of nutrients. Water temperature (T), dissolved oxygen (DO), and salinity were measured *in situ* using a CTD profiler.

2.2 eDNA extraction, PCR amplification, and sequencing

Total DNA was isolated from the seawater samples using the DNeasy PowerWater Kit (Qiagen, Germany) following the manufacturer's protocol, and stored at -80°C until further processing. The concentration and purity of the extracted DNA were evaluated with a NanoDrop NC2000 spectrophotometer (Thermo Fisher Scientific, USA). Two universal MiFish primer sets (MiFish-U and MiFish-E) were used in a multiplex PCR approach to amplify the hypervariable region of the mitochondrial 12S rRNA gene from a wide range of fish taxa present in the eDNA samples (Miya et al., 2020). Multiplex PCR was carried out in a 50 μl reaction system containing



25 μ l of Taq 2 \times Master Mix (Vazyme), 20 μ l of ddH₂O, 1 μ l each of forward and reverse primers (MiFish-U-F: 5'-GTCGGTA AACTCGTGCCAGC-3', MiFish-U-R: 3'-GTTTGACC CTAATCTATGGGGTGATAC-5', MiFish-E-F: 5'-GTTGGTAAATC TCGTGCCAGC-3', and MiFish-E-R: 3'-GTTTGATCCTAATCTA TGGGGTGATAC-5'), and 1 μ l of template DNA. The thermal cycling conditions consisted of an initial denaturation step at 94 °C for 2 min, followed by 30 cycles of denaturation at 98 °C for 5 s, annealing at 55 °C for 10 s, and extension at 72 °C for 10 s, with a final elongation at 72 °C for 5 min (Miya et al., 2020). After amplification, PCR products were subjected to electrophoresis on 1% agarose gels to verify the amplicon size. Samples exhibiting a clear and intense band within the expected size range of 163–185 bp were chosen for subsequent procedures. High-throughput sequencing was performed by Shanghai Personalbio Biological Company. Sequencing libraries were constructed with the TruSeq Nano DNA LT Library Prep Kit in accordance with the manufacturer's guidelines, and library quality was evaluated using an Agilent Bioanalyzer and the Promega QuantiFluor system. Deep sequencing was executed on the Illumina NovaSeq platform with the NovaSeq 6000 SP Reagent Kit.

2.3 Bioinformatics

Bioinformatics analyses were performed with QIIME2 version 2019.4 (Bolyen et al., 2019), with modifications adapted from the official tutorial (<https://docs.qiime2.org/2019.4/tutorials/>). Initially, raw sequence data were demultiplexed using the demux plugin. Primer sequences were then trimmed with the cutadapt plugin to remove any residual primers that might otherwise interfere with subsequent analytical steps (Martin, 2011). Sequence quality control, denoising, merging, and chimera removal were performed using the DADA2 plugin (Callahan et al., 2016). Quality filtering parameters—including truncLen, maxEE, and truncQ—were applied to ensure that only high-confidence amplicon sequence variants (ASVs) were retained. Paired-end reads were merged, and ASVs were inferred through the DADA2 denoising process, with singleton sequences removed (Callahan et al., 2016). Subsequently, taxonomic annotation of these ASVs was conducted by aligning them against reference sequences from the NCBI (<https://www.ncbi.nlm.nih.gov>) database. For each assignment, multiple alignment criteria were adopted to identify the optimal match, including alignment length, percent identity, number of mismatches within the aligned segment, bit-score and E-value. A composite score derived from these criteria was used to select the best match, with final taxonomic labels assigned preferentially to sequences exhibiting 100% identity and the lowest E-value (Callahan et al., 2016).

2.4 Statistical analysis

2.4.1 Comparison and stability of fish community

All statistical analyses were conducted in R Studio Version 4.3.3 (Team, 2014). Species richness, representing TD α , was estimated across various areas using the R package vegan. The Shapiro–Wilk test was employed to assess normality of the data, and variations

between areas were examined using the Wilcoxon rank-sum test (Jiang et al., 2024; Zhong et al., 2022). Data on the functional traits of fish species were collected from FishBase (<https://fishbase.org/search.php>). These five traits reflect multiple ecological dimensions, including vertical distribution, habitat preference, trophic level, migratory behavior, and maximum body length (Supplementary Table S1) (Aglieri et al., 2021; Clay et al., 2025; Coleman et al., 2015). They are indicative of fundamental ecological characteristics such as mobility, microhabitat use, behavioral strategy, diet, and life history (Cantera et al., 2023; Gomes et al., 2023). To evaluate beta diversity, the original species abundance matrix was first converted into a binary presence-absence matrix. Functional diversity of fish assemblages was analyzed using the mFD package in R (Magneville et al., 2022). Trait information was summarized by integrating data on fish abundance, trait values, and trait categories. A standardized interspecies distance matrix was then calculated based on Gower distance. The quality of the functional space was assessed, and its stability was visualized to evaluate robustness. Species coordinates within functional space were obtained, and correlations between species and principal coordinates were examined (Magneville et al., 2022). Finally, multidimensional functional diversity indices were computed, with functional richness used as a measure of functional alpha diversity (FD α). Convex hull plots were generated to visualize the distribution of species within the functional space. Beta diversity was subsequently partitioned into its three components—total beta diversity (β_{jac}), turnover (β_{jtu}), and nestedness (β_{jne})—based on the Jaccard dissimilarity index (Wu et al., 2022). Additionally, Pearson correlation analysis was performed to examine the relationship between taxonomic diversity (TD) and functional diversity (FD) (Jiang et al., 2024). The single-trait-based community-weighted means (CWM) was calculated for each trait through the FD package in R:

$$CWM_{jk} = \sum_{i=1}^n P_{ik} \times t_{ij}$$

where P_{ik} is the relative abundance of species i in community k , t_{ij} is the trait value of trait j for species i , and n is the total number of species. For the five continuous traits, the CWM represents the abundance-weighted mean trait value across all species in the community. For each category of the three categorical traits, CWM corresponds to the relative abundance of species (Xia et al., 2025).

Functional entities (FEs), defined as unique combinations of functional traits within the fish community, were identified based on trait data using the “species_to_FE” function in R (McKinley et al., 2023). Three components of functional vulnerability—functional redundancy, functional over-redundancy, and functional sensitivity—were calculated according to the following formulas:

$$\text{Functional redundancy} = \frac{S}{FE}$$

Functional over – redundancy

$$= \frac{\sum_{i=1}^{FE} \min[(\max(n_i, Fred)) - Fred, 1]}{FE}$$

$$\text{Functional sensitivity} = \frac{FE - \sum_{i=1}^{FE} \min(n_i - 1, 1)}{FE}$$

In these formulas, S denotes species richness and n_i represents the number of species within the i_{th} functional entity (FE). Functional redundancy ranges from 1 to S : a value of 1 indicates no redundancy among functional entities, while a value of S implies that all species belong to a single FE. Functional sensitivity ranges from 0 to 1, where 0 corresponds to complete redundancy across all FEs, and 1 indicates the complete absence of redundancy. Both functional sensitivity and over-redundancy are classified as low (< 0.5), medium ($0.5-0.75$), or high (> 0.75). Similarly, functional redundancy is categorized as low (< 1.5), medium ($1.5-1.75$), or high (> 1.75) (McKinley et al., 2023).

2.4.2 Construction of co-occurrence network

To investigate the co-occurrence patterns of specialist and generalist species within the community, a species interaction network was constructed using the *igraph* package in R (Sun et al., 2024). Pairwise associations between species were evaluated through Pearson correlation analysis, with edges included only for correlations meeting a threshold of $r > 0.6$ and a significance level of $p < 0.05$. Key nodes within the network were classified as module hubs, connectors, or network hubs, while peripherals were considered non-key nodes (Deng et al., 2012). The clustering coefficient and modularity of the network were calculated to infer interspecific interactions among fish species. To assess the contributions of specialist, generalist, and neutral species to the community structure, a similarity percentage (SIMPER) analysis was applied based on the Bray–Curtis similarity index (Clarke, 1993). This method quantifies the contribution of each species to the overall dissimilarity between assemblages (Baldwin et al., 1998). All analyses were performed using the *vegan* package in R, which facilitated pairwise comparison between assemblages and identification of taxa with significant influence on community differences (Sun et al., 2020).

2.4.3 Neutral community model for fish community

The NCM was used to assess the potential contribution of stochastic processes to the community assembly by characterizing the relationship between species detection frequency and relative abundance (Sloan et al., 2006). The model was fitted via nonlinear least squares regression, with all parameters and confidence intervals estimated from 1,000 bootstrap iterations. Species were categorized based on their position relative to the 95% confidence interval: those above the upper limit, below the lower limit, or within the interval (Chen et al., 2019). Model implementation was carried out using the *minpack.lm* package in R, where m represents the migration rate and N_m indicates the metacommunity size. The overall fit of the model was evaluated using the R^2 value; a higher R^2 suggests that stochastic processes play a dominant role in community assembly, whereas deterministic factors are less influential (Chen et al., 2019; Li et al., 2024).

To assess the effects of the environmental factors on alpha diversity, correlations were examined using Pearson correlation analysis and the Mantel test (Sun et al., 2024). Subsequently, structural equation modeling (SEM) was applied to further investigate the direct and indirect influences of the environmental factors on biodiversity indices. The *plspm* function in R was used to analyze the impacts of the environmental variables on $TD\alpha$ and $FD\alpha$ across the study period (Evermann and Tate, 2016).

2.4.4 Hierarchical modeling of species communities analysis

To compare taxa composition across the different areas (inshore, midshore, offshore, and principal axis areas), the taxa occurrence matrix for each sample was analyzed. Hierarchical modeling of species communities (HMSC) was applied in combination with eDNA-derived presence–absence data (Polanco-Fernandez et al., 2022; Ovaskainen and Abrego, 2020). HMSC, as a joint species distribution model (JSDM), accounts for hierarchical structure to better capture taxa responses to environmental covariates (Warton et al., 2015). To reduce bias from rare or ubiquitous taxa, species detected in fewer than three filters or in more than $n-2$ filters were excluded, where n represents the total number of samples (filters), with each filter corresponding to one sampling site (Ovaskainen and Abrego, 2020). The resulting presence–absence matrix served as the response variable, with offshore distance included as a fixed effect. Models were implemented in the *Hmsc* R package with default priors (Ovaskainen and Abrego, 2020; Rozanski et al., 2024). Parameter estimation used four Markov Chain Monte Carlo (MCMC) chains of 37,500 iterations each, discarding the first 12,500 as burn-in and thinning by 100, yielding 1000 posterior samples per chain (Abrego et al., 2024). Model performance for each species was evaluated by comparing observed and predicted occurrences using the area under the receiver operator curve (AUC) and Tjur R^2 (Rozanski et al., 2024). Finally, pairwise area comparisons were conducted to calculate the proportion of species showing positive or negative responses to inshore conditions, with 95% credible intervals for model coefficients.

3 Results

3.1 Comparison and diversity of fish community

Taxonomic classification of the ASVs identified 93 families, 167 genera, and 206 distinct fish species (Supplementary Table S2). The $TD\alpha$ index indicated no significant differences among the four different areas of the TWS ($p > 0.05$, Supplementary Figure S1). Functional diversity analysis revealed that turnover was the dominant process underlying functional beta diversity (Figures 2a, b), with its contribution consistently exceeding that of nestedness. A significant correlation was found between taxonomic and functional alpha diversity, indicating a strong

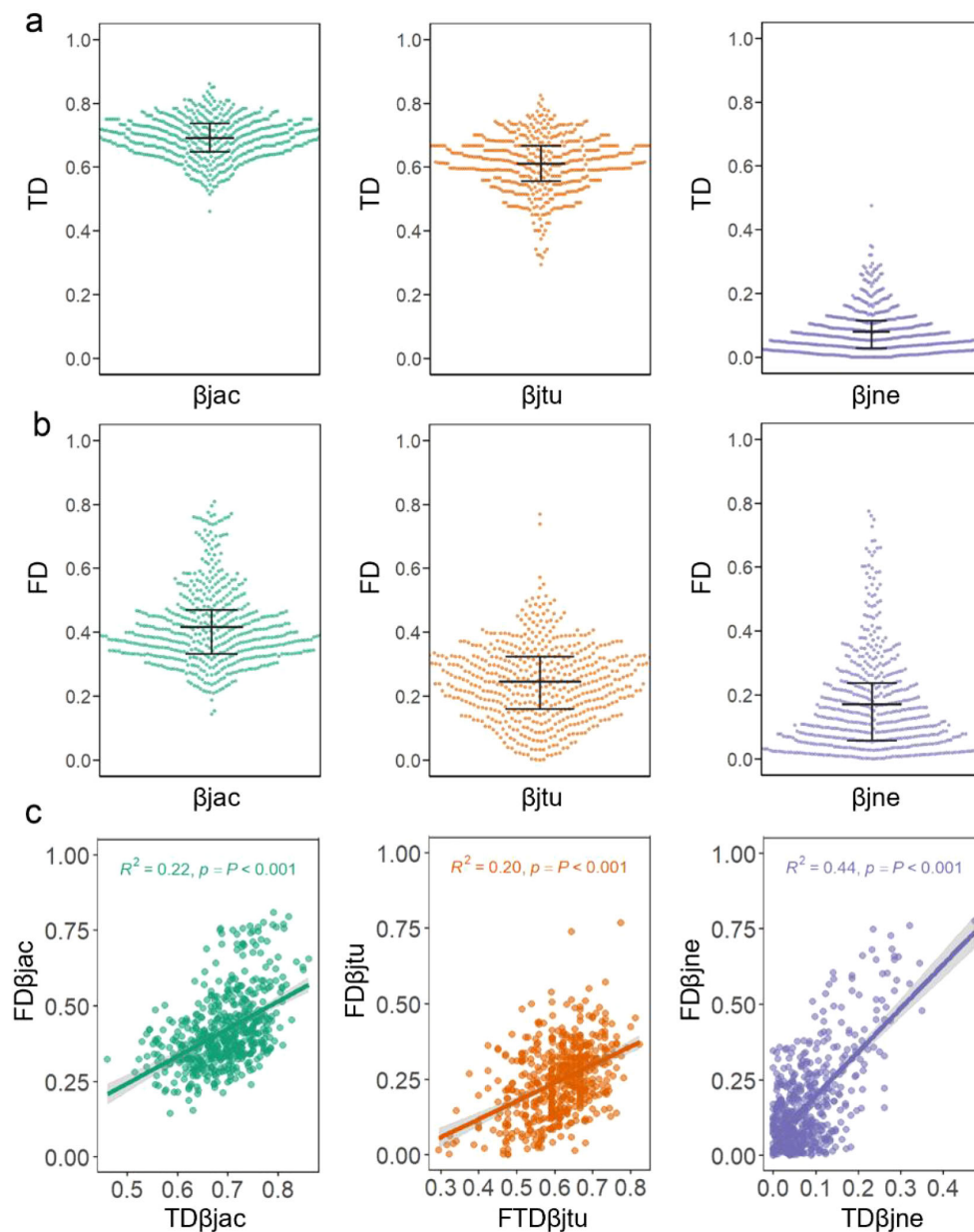


FIGURE 2

Components of taxonomic diversity (a) TD β_{jac} , TD β_{jtu} , TD β_{jne} ; and functional diversity (b) FD β_{jac} , FD β_{jtu} and FD β_{jne} . (c) Correlations between TD, FD and their components at beta diversity.

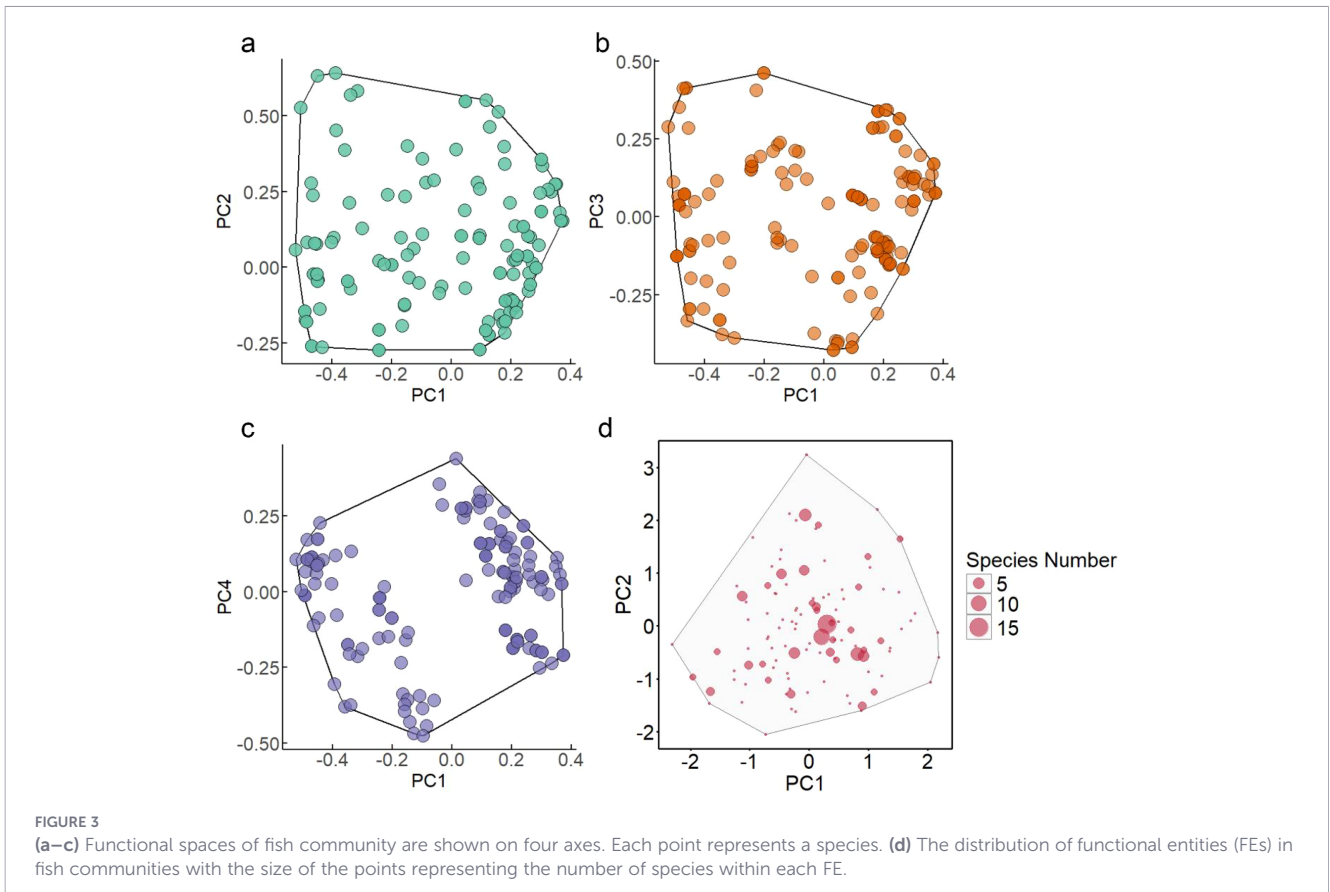
linkage between species richness and functional trait composition in the examined communities (Supplementary Figure S2). Similarly, in TWS, significant correlations were detected between taxonomic and functional beta diversity, as well as between their respective turnover and nestedness components (Figure 2c).

3.2 Community stability and co-occurrence patterns of fish species

The functional structure of the fish community showed an uneven distribution of species across the four-dimensional functional space, which gradually contracted over the study

period (Figures 3a–c). Among the 206 fish species identified, 111 functional entities (FEs) were delineated. Species distribution among FEs was highly skewed: 78 FEs contained only one species, while 33 FEs displayed functional redundancy. Overall, most FEs showed no redundancy, and the distribution of species across FEs remained markedly uneven (Figure 3d). The functional redundancy of the fish community in TWS was moderate with a value of 1.739, whereas functional over-redundancy and functional sensitivity were both low, with values of 0.179 and 0.297.

Co-occurrence network analysis of the fish community revealed a distinct modular structure. Species within individual modules were tightly interconnected, whereas links between different



modules were sparse. This high modularity and weak inter-module connectivity resulted in a relatively loose overall network topology in TWS (Figure 4a). The co-occurrence network in the midshore and offshore areas exhibited higher modularity (Table 1; Figures 4c, d). The inshore and principal axis areas exhibited lower modularity while also having a higher clustering coefficient. In contrast, the co-occurrence network in the inshore area and principal axis displayed an opposite pattern, with nodes remaining connected (Figures 4b, e).

3.4 Ecological processes that structure fish community composition

NCM and SEM were employed to assess the contributions of stochastic and deterministic processes to the variation in fish community composition. The NCM effectively characterized the relationship between species occurrence frequency and relative abundance, explaining 55.9% of the variation in fish community assembly in the TWS (Figure 5a), indicating a substantial

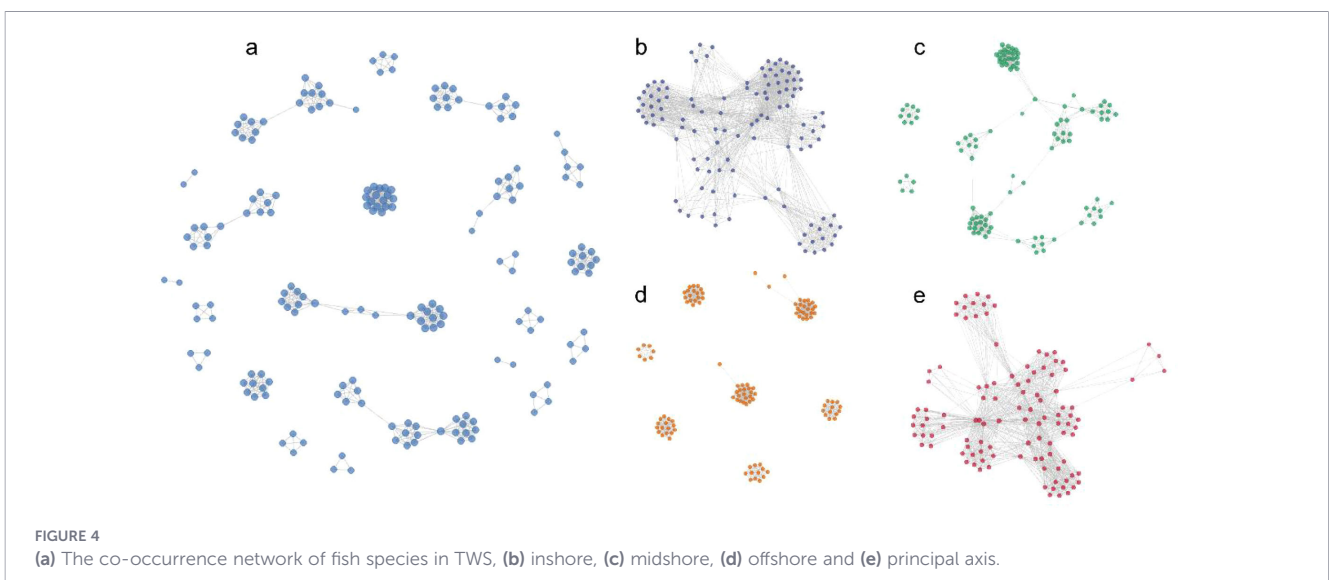


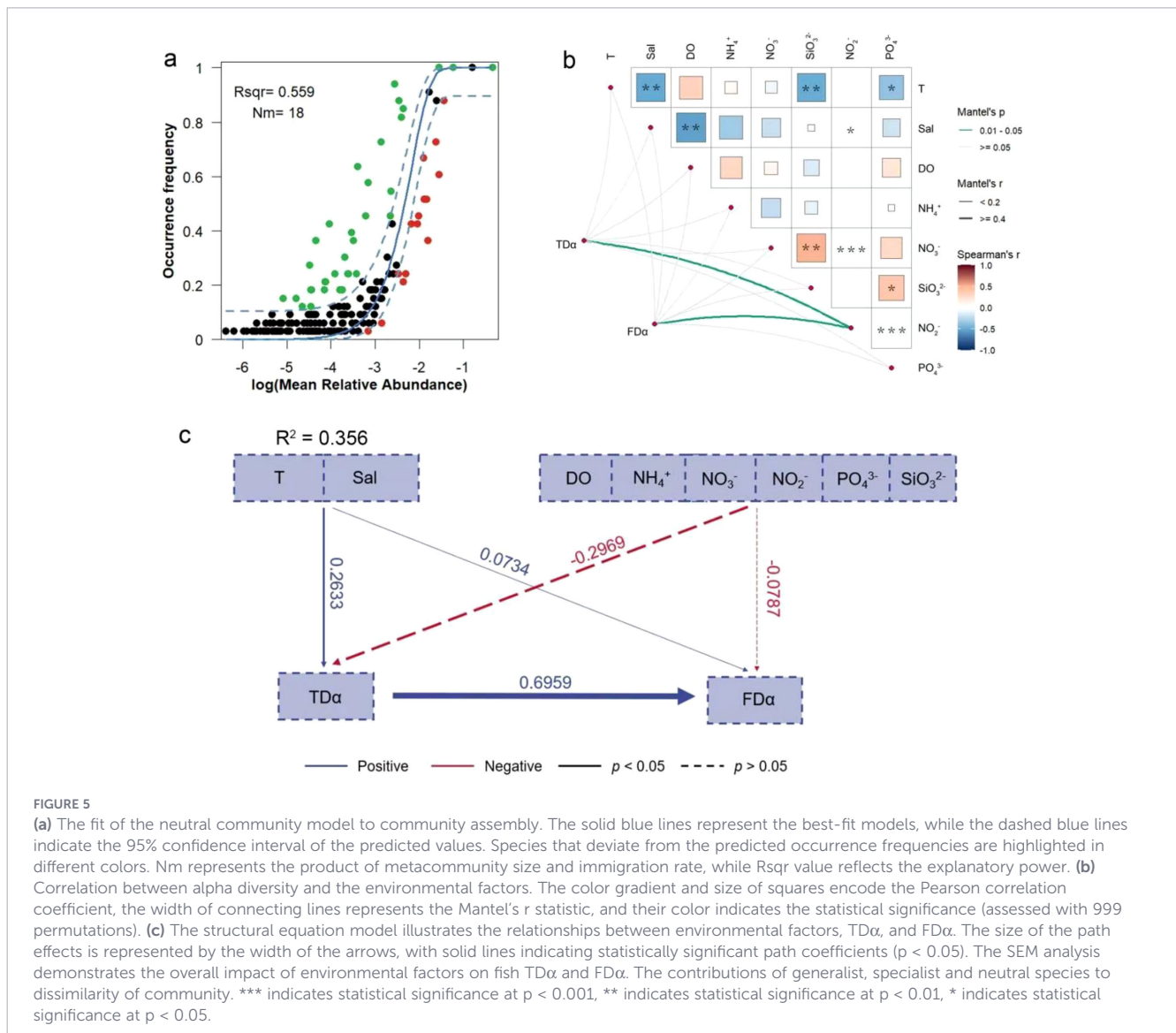
TABLE 1 Co-occurrence network parameters in the different areas.

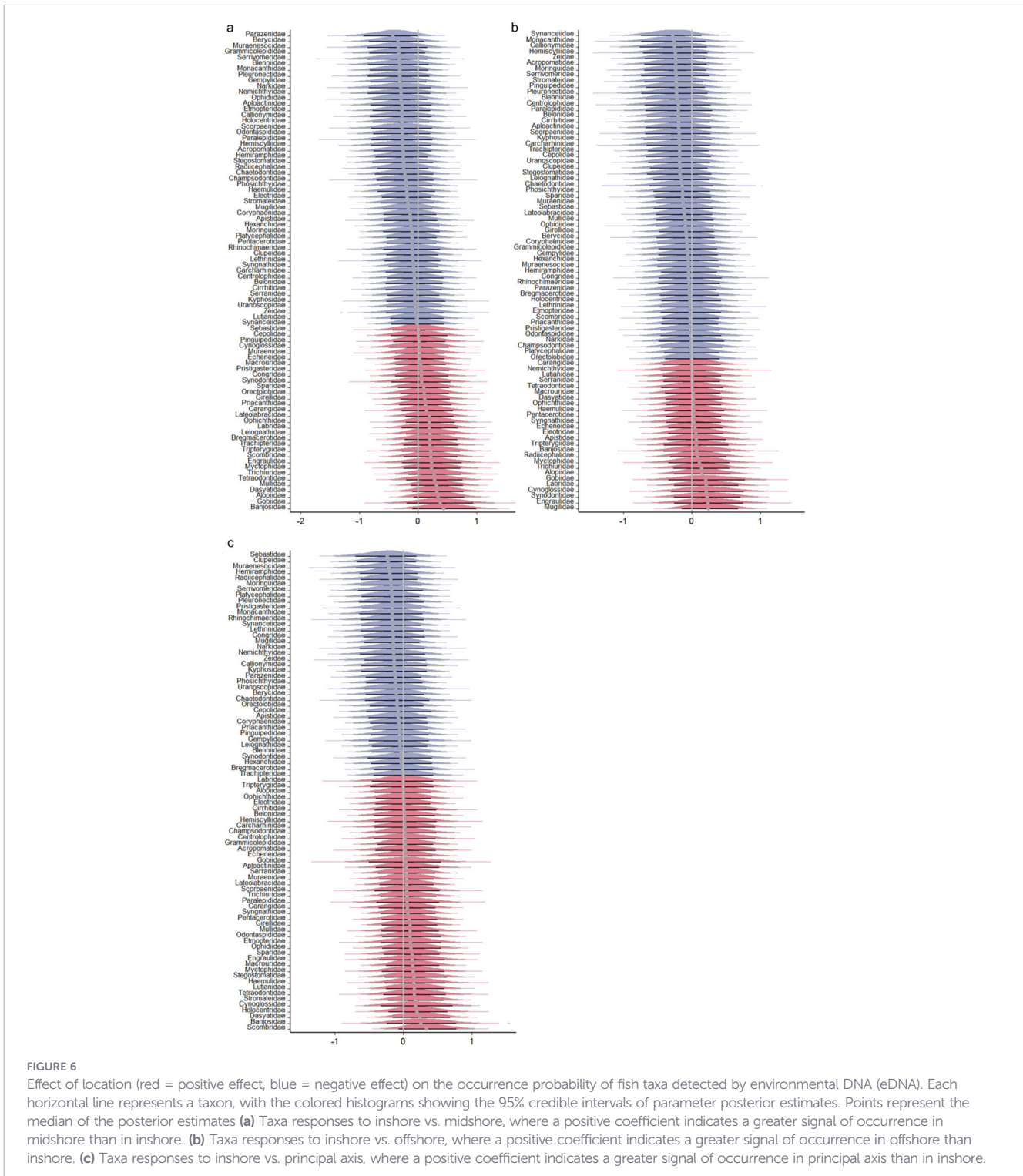
Area	Clustering coefficient	Modularity
Inshore	0.9344158	0.394639
Midshore	0.7424894	0.742325
Offshore	0.647308	0.810041
Principal axis	0.9894648	0.45625

contribution of stochastic processes. To further examine species that deviated from neutral expectations, the GPD parameter yielded $\xi < 0$, indicating that the distribution of species falling outside the NCM confidence interval followed a bounded short-tailed pattern. The estimated GPD parameters showed a negative shape parameter and a moderate scale parameter, with ξ equal to -0.796 ± 0.21 and σ equal to 0.483 ± 0.11 , indicating that deterministic processes such as environmental filtering and biotic interactions contributed to species distributions in the TWS. Mantel tests identified a significant effect of NO_2^- on both $\text{TD}\alpha$ and $\text{FD}\alpha$. SEM further

revealed that temperature and salinity exerted significant positive effects on $\text{TD}\alpha$ and $\text{FD}\alpha$ (Figure 5b), whereas chemical environmental factors generally had negative impacts on $\text{TD}\alpha$ and $\text{FD}\alpha$ (Figure 5c). These results indicated that deterministic environmental factors influence community assembly through different pathways. Temperature and salinity exerted direct positive effects on taxonomic diversity, which in turn directly promoted functional diversity. In contrast, NO_2^- showed significant negative effects on both taxonomic and functional diversity, indicating its role as a negative deterministic environmental driver in shaping community assembly.

The HMSC showed good discriminatory performance, with an average AUC of 0.938, whereas the Tjur R^2 value of 0.102 highlights the contribution of additional unmeasured variables and latent factors beyond offshore distance. Results from the HMSC applied to the taxa revealed distinct regional occurrence patterns among most taxa (Figures 6a, b). Specifically, the majority of taxa showed a higher probability of occurrence in inshore areas compared to midshore and offshore areas. Furthermore, along the principal

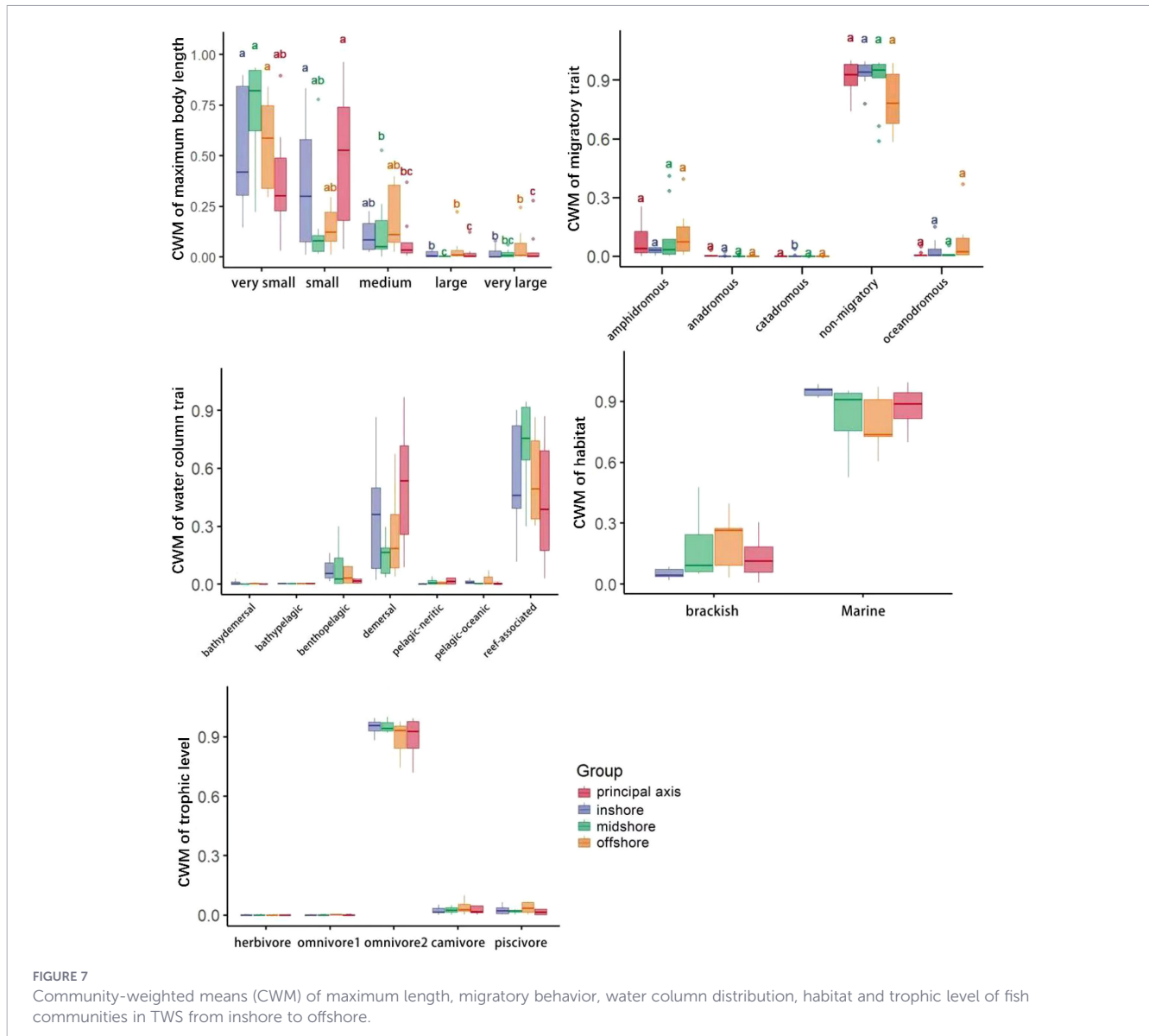




axis, taxa generally exhibited higher occurrence probabilities in inshore areas. Several families—including Parazenidae, Synanceiidae, Sebastidae—demonstrated significantly higher occurrence probabilities the inshore area. HMSC analysis showed that the occurrence probabilities of taxa in the inshore and principal axis areas were similar (Figure 6c). Specifically, Banjosidae were more likely to occur in the midshore area, Mugilidae in the offshore area, and Scombridae in the principal axis area.

3.5 Response of CWM to offshore distance

The fish community in TWS was dominated by species with very small (< 10 cm) and small (10–30 cm) body lengths, whereas large (50–100 cm) and very large (> 100 cm) species were relatively scarce (Figure 7). Among the trophic groups, omnivore fishes accounted for a higher proportion. Overall, the community was mainly composed of non-migratory reef-associated fishes. The



effect of offshore distance on community structure was primarily reflected in the changes of very small body length species whereby their abundance decreased with increasing offshore distance, while the proportions of small and medium-sized species increased. From midshore to offshore, benthic species decreased in number, and reef-associated fishes declined in proportion (Figure 7).

4 Discussion

This study utilized eDNA metabarcoding to investigate fish diversity in the TWS from multiple perspectives, effectively overcoming the limitations of traditional approaches that assess fish communities from a single dimension. By comprehensively examining both taxonomic and functional α and β -diversity, the research provides an integrated understanding of spatial patterns in fish community structure within the TWS. Recognizing that a single redundancy metric cannot fully represent community stability, this

study further incorporated functional redundancy, over-redundancy, and functional sensitivity to provide a more holistic evaluation of community vulnerability. Additionally, the mechanisms underlying fish community assembly and the effects of offshore distance on species traits and spatial distribution were explored, thereby addressing key knowledge gaps in our understanding of fish community dynamics in the TWS.

4.1 Stability and assembly patterns of fish community

The use of eDNA metabarcoding allowed for a more comprehensive assessment of fish diversity compared with previous research in TWS. Decomposition of taxonomic and functional β -diversity revealed that $TD\beta_{jtu}$ exceeded $TD\beta_{jne}$, suggesting that fish community patterns were primarily driven by species turnover rather than nestedness. In contrast, although $FD\beta_{jtu}$ and $FD\beta_{jne}$ differed less markedly, $FD\beta_{jne}$ remained lower than $FD\beta_{jtu}$, indicating that functional β -diversity patterns

were influenced by both nestedness and turnover, with turnover contributing more prominently. These findings align with those of Ni et al. (2020), supporting the notion that taxonomic diversity is mainly determined by turnover (Ni et al., 2020). This pattern likely reflects the combined effects of dispersal limitation, local environmental conditions, and regional drivers (Gianuca et al., 2017). The relatively low migration rate observed in TWS may result from a limited dispersal capacity and reduced habitat connectivity, which restrict species movement. High dispersal rates typically reduce turnover significance by homogenizing community composition (Fu et al., 2019), whereas the low dispersal efficiency in TWS reinforces the role of turnover.

Strong correlations between taxonomic and functional diversity at both alpha and beta levels indicated a close linkage between species richness and functional diversity across ecological scales. SEM analysis further confirmed a significant positive effect of taxonomic diversity on functional diversity, suggesting that changes in species composition can directly drive alterations in community functioning. This underscores the ecological importance of maintaining species richness to sustain functional diversity.

Functional entities (FEs) were closely tied to species richness. Although most FEs remained stable, a notable fraction was supported by a single species, and this implies potential ecosystem vulnerability. While a higher species diversity may partially buffer against functional loss, ecosystem fragility may still exceed expectations even in species-rich systems (Mouillot et al., 2014). Coral reef ecosystems, as some of the most species-rich marine systems globally, often exhibit high functional redundancy accompanied by strong functional over-redundancy, resulting in many functionally vulnerable entities being supported by a single species (Mouillot et al., 2014). This finding indicates that high biodiversity does not necessarily confer high functional resilience. In the TWS, the observed moderate functional redundancy and low functional over-redundancy suggest a limited capacity to buffer against species loss and disturbance. A lower functional redundancy implies that species loss due to environmental disturbances could substantially reduce functional diversity, exacerbating ecological vulnerability (Bellwood et al., 2003; Bihn et al., 2010). Low FR suggests species occupy a wider array of ecological niches, a notion supported by the observed low FOR (Gajdzik et al., 2018). Despite a low functional redundancy, the fish community still maintained a considerable proportion of ecologically unique species occupying distinct roles, indicating high niche differentiation and functional complementarity under current conditions (McKinley et al., 2023). However, under combined environmental pressures, these unique species may be particularly vulnerable. In marine ecosystems, the loss of such species can lead to immediate and potentially irreversible functional consequences due to a low likelihood of replacement (Fetzer et al., 2015; McKinley et al., 2023). When community functions are supported by only a few species, a greater number of ecological niches become directly exposed to the risk of species loss. In the TWS, under disturbance conditions, the loss of even a

small number of functionally unique species may lead to rapid declines in functional diversity, thereby increasing the system sensitivity to environmental perturbations. The coexistence of low FR and low FOR indicates efficient resource use with minimal interspecific competition (Hooper et al., 2012; Loreau et al., 2001). In TWS, fish species and FEs were unevenly distributed within functional space (Figures 3c, d), reflecting moderate FR, low FOR, and an overall high vulnerability community structure. The functional redundancy observed in the TWS is comparable to values reported for other continental shelf and coastal systems. Studies from the Barents Sea have shown that fish community functions are supported by a limited subset of species, resulting in moderate functional redundancy and reduced buffering capacity against environmental change. Consequently, despite relatively stable overall species richness, such systems remain sensitive to disturbances. Similar patterns have also been reported in coastal systems such as the Pearl River Estuary, where fish communities exhibit moderate to high functional redundancy but remain functionally vulnerable due to low functional diversity. In the TWS, the combination of moderate functional redundancy, low functional over-redundancy, and relatively low functional sensitivity indicates that key ecosystem functions are maintained by a small number of functionally similar species with limited replacement capacity. Compared with coral reef ecosystems, TWS fish communities lack sufficient buffering capacity against species loss or environmental disturbance. Together, these patterns suggest that, although functional redundancy in the TWS is moderate, its functional resilience is limited, making the system more susceptible to ongoing environmental change and anthropogenic pressures.

In natural ecosystems, organisms rarely exist in isolation, instead forming intricate co-occurrence patterns that can enhance community resilience. Species co-occurrence is a key aspect of community ecology, and analyzing these patterns provides insights into coexistence mechanisms shaping fish communities (Wang et al., 2020). Significant positive or negative correlations indicate species aggregation or segregation, respectively (Buckley et al., 2016). In the TWS, positively correlated links suggest a stronger tendency for co-occurrence rather than mutual exclusion under environmental fluctuations (Sun et al., 2024). Within networks, species belonging to the same module exhibit strong internal interactions, whereas interactions between modules are weaker (Bascompte et al., 2003). Our results revealed distinct modularity in TWS co-occurrence networks, consistent with findings from Mas et al. (2022) in the Parana River (Mas et al., 2022). High modularity generally reduces network robustness to disturbances (Nuwagaba et al., 2017), highlighting its importance in shaping ecological stability (Borthagaray et al., 2014).

4.2 Mechanisms of fish assembly

Environmental factors are key drivers of fish community assembly. Variables such as temperature, salinity, and electrical conductivity significantly shape the structure and spatial distribution of fish communities (Marques et al., 2026). For

instance, salinity, elevation, and chlorophyll-*a* have been identified as major factors influencing fish distribution (Ding et al., 2025). Although environmental factors can also affect the dynamics of eDNA, including its release, transport, degradation, and detection probability, multiple studies have demonstrated that these factors do not necessarily reduce detection success (Yates et al., 2023). Natural levels of ultraviolet radiation and filter-feeding activity have no measurable impact on eDNA-based detection rates, and temperature has been shown to have no significant effect on the degradation or detection of eDNA in marine and tropical environments (Machler et al., 2018; Robson et al., 2016). Although environmental parameters can accelerate molecular degradation, they generally do not affect the overall reliability of eDNA detection under natural conditions (Pont, 2024).

Hydrodynamic mixing is an important factor to consider when using eDNA to assess biodiversity, particularly in nearshore and coastal systems. Multiple studies have shown that although tidal exchange and current-driven transport can influence eDNA distribution over short time scales, their spatial effects are often limited. Jeunen et al. demonstrated that eDNA signals remained spatially distinct between marine habitats separated by less than 5 km, indicating that water mixing did not homogenize community signals (Jeunen et al., 2019). At broader spatial scales, the effective integration distance of eDNA typically ranges from several hundred meters to a few kilometers, depending on hydrological connectivity (Littlefair et al., 2023). Although hydrodynamic processes may locally influence eDNA signals, eDNA in marine and coastal environments generally retains strong spatial specificity. Therefore, the sampling distances adopted in this study, with an average inter-station distance of 24.9 km, are considered sufficient to minimize the confounding effects of hydrodynamic mixing on the detection of community turnover.

To identify the dominant processes governing fish assembly, this study integrates the neutral theory and network topology indices to elucidate the mechanisms underlying fish community structuring in the TWS (Liao et al., 2016; Sun et al., 2024). Both stochastic and deterministic processes exerted comparable influences on community assembly, suggesting that both processes contributed similarly to the structuring of the fish community. Given the relatively limited research on TWS fish community assembly, these findings provide valuable insights into the ecological processes shaping fish communities. The fish community does not remain in a stable assembly state, but rather transitions between deterministic and stochastic process (Strange et al., 1993). The NCM analysis in TWS indicated that both deterministic (NO_2^- and species interactions) and stochastic processes (births, deaths, and immigration) jointly governed fish community assembly (Chen et al., 2019). Our results differ from those of Chen et al., who reported that fish communities in the Pearl River Estuary are primarily driven by stochastic processes (Chen et al., 2024). The shape parameter ξ further elucidated the ecological mechanisms behind these deviations. The species that fell outside the NCM confidence intervals exhibited a bounded distribution, as

indicated by $\xi < 0$. Additionally, the scale parameter suggested that these species deviated substantially from neutral expectations, supporting the interpretation that deterministic processes played an important role in shaping their distribution. Topological indices and mantel analysis showed that the fish community composition is primarily driven by deterministic processes, including environmental factors (NO_2^-) and species interactions.

4.3 Community composition and traits across different areas

Modularity and clustering coefficient are commonly used as essential indicators for characterizing ecological networks at the community scale (Berry and Widder, 2014; Wu et al., 2020a). Generally, higher modularity reflects a more fragmented network structure (Wang et al., 2023). In the TWS, modularity values in the midshore and offshore regions were greater than those in the inshore and principal axis regions, suggesting that fish communities in the former areas exhibited a more fragmented structural pattern. Except for the inshore region, all modularity values in TWS exceeded the threshold of 0.4, indicative of significant modular structures, which in turn imply strong network fragmentation and weakened species interactions (Wang et al., 2023). The clustering coefficient provides a measure of network cohesiveness, where higher values denote stronger interspecific connections. The relatively lower clustering coefficients in the midshore and offshore areas indicate reduced cohesiveness and weaker species interactions. Such patterns are likely linked to habitat heterogeneity, as the fragmented habitat structure of TWS—exacerbated by navigation and fishing activities—has intensified habitat degradation and increased environmental stress (Wu et al., 2020b).

The results demonstrated that $\text{TD}\alpha$, Shannon, Simpson, and $\text{FD}\alpha$ indices showed no significant differences across areas from inshore to offshore, which contradicted our initial hypothesis. However, HMSC and CWM analyses revealed that offshore distance significantly affected trait variation and species distribution in fish communities. In the inshore region, Parazenidae species were mostly small to medium-sized, laterally compressed, benthic or near-bottom fishes feeding on small crustaceans and fishes; Synanceiidae were benthic ambush predators often buried in reefs or sandy-mud bottoms, preying on crustaceans and small fishes, and commonly associated with coral reefs; Sebastidae fed mainly on benthic invertebrates and small fishes. In the midshore region, Banjosidae were small coastal schooling fishes with broad diets including plankton and small invertebrates. In the offshore region, Mugilidae were euryhaline fishes and typical commercial species. In the principal axis region, Scombridae were fast-swimming pelagic carnivores feeding on small fishes and cephalopods, representing important migratory commercial species. The Taiwan Strait, located within the Kuroshio Triangle, provides a critical habitat for migratory species due to its distinctive current regimes and bathymetric conditions (Hsiao et al., 2021; Tiedemann and Brehmer, 2017).

Upwelling, characterized by high net primary productivity, along with cold, nutrient-rich features, promote zooplankton proliferation. This, in turn, supports forage fish communities and attracts large numbers of cold-water pelagic predators, particularly those from the family Scombridae, which aggregate in these productive waters (Kiyota et al., 2020; Ware and Thomson, 2005). Additionally, the Taiwan Strait is influenced by river estuaries, where freshwater inputs drive physical changes in estuarine and coastal environments, directly or indirectly affecting marine species (Broadley et al., 2022), and contributing to variability in species movement and migration (Caddy, 2020).

Fish community structure in the TWS was predominantly composed of species with very small and small length. Hu et al. (2015) analyzed the life-history variations of fish from the coast of Fujian to the coast of Taiwan Island and reported that, under fishing pressure, fish communities tend to become dominated by smaller-bodied species (Hu et al., 2015). In unstable and highly stressed estuarine environments, fish species that mature rapidly, have short life cycles, and possess smaller body sizes are more likely to prevail (Teichert et al., 2017). As the distance from the coast increases, the proportion of very small-sized fish declines, while small and medium-sized species gradually becoming more dominant. From the midshore to offshore regions, the abundance of benthic fish decreases, accompanied by a decline in the proportion of coral reef-associated species. Kornis et al. (2017) reported that small-bodied, bottom-oriented species preferentially inhabit shallow waters where resource availability is higher (Kornis et al., 2017). Overall, the results of CWM were consistent with the fish community patterns revealed by the HMSC analysis, indicating a concordant reflections of structural differences across the four different areas.

5 Conclusion

This study demonstrates that eDNA metabarcoding is a reliable approach for assessing species composition, functional structure, and assembly mechanisms of fish communities in TWS. Our findings revealed that fish communities in the TWS were generally high vulnerability, exhibiting moderate redundancy, uneven functional space distribution, high modularity, and weak interspecific interactions. Community assembly was jointly driven by stochastic and deterministic processes, with deterministic processes primarily influenced by the environmental factor NO_2^- and species interactions. While $\text{TD}\alpha$ and $\text{FD}\alpha$ showed no significant differences from estuarine to offshore areas, fish communities in the inshore and principal axis areas exhibited higher aggregation but lower modularity compared to the other areas. HMSC and CWM further indicated distributional and trait differences of fishes from the estuarine to inshore areas, highlighting species-specific environmental preferences. Overall, fish communities in TWS were dominated by very small and small body-length traits, with reef-associated species mainly distributed in the inshore and midshore areas.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: <https://www.ncbi.nlm.nih.gov/sra/PRJNA1431738>.

Author contributions

WH: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft. HH: Conceptualization, Data curation, Investigation, Methodology, Writing – review & editing. LW: Conceptualization, Data curation, Formal analysis, Methodology, Writing – review & editing. DO: Conceptualization, Formal analysis, Investigation, Validation, Writing – review & editing. JW: Data curation, Formal analysis, Methodology, Writing – review & editing. RH: Writing – review & editing. YZ: Data curation, Investigation, Methodology, Writing – review & editing. JQ: Data curation, Methodology, Writing – review & editing. WL: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing – review & editing. KL: Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing. SP: Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing.

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Conflict of interest

The authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2026.1761251/full#supplementary-material>

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