Journal of Oceanology and Limnology

https://doi.org/10.1007/s00343-026-5387-y

Research Paper

Spatial and environmental factors drive the distribution patterns and community assembly of planktonic ciliates in the nearshore waters of southeastern China*

Yonghua ZHOU, Yifan GU, Wenjing ZHANG**

State Key Laboratory of Marine Environmental Science, Xiamen Key Laboratory of Urban Sea Ecological Conservation and Restoration, College of Ocean and Earth Sciences, Xiamen University, Xiamen 361102, China

Received Oct. 6, 2025; accepted in principle Jan. 5, 2026; accepted for publication Feb. 28, 2026

© Chinese Society for Oceanology and Limnology, Science Press and Springer-Verlag GmbH Germany, part of Springer Nature 2026

Abstract Planktonic ciliates are ecologically important protists in marine ecosystems, yet their distribution patterns and assembly mechanisms at the regional scale remain insufficiently understood in dynamic nearshore ecosystems. Here, we employed 18S rRNA metabarcoding of 578 water samples collected during spring from five nearshore regions of southeastern China to characterize planktonic ciliate communities, aiming to unveil their distribution patterns, community stability, and assembly processes under diverse environmental conditions. The results reveale significant spatial heterogeneity in ciliate community composition, with Spirotrichea dominating across regions. Ciliate diversity peaked in Dongshan Bay and decreased northward. Environmental factors played a dominant role in shaping ciliate community structure, with temperature identified as the most critical driver. Notably, this pattern was consistent in both aloricate and loricate (tintinnid) ciliate communities. Furthermore, environmental factors were the primary drivers in Dongshan Bay, Pingtan, and the Minjiang estuary, whereas spatial factors played a more prominent role in Sansha Bay. Network analysis indicated higher structural stability in Dongshan Bay and Sansha Bay, in contrast to Minjiang estuary and Pingtan. The neutral community model revealed significant regional differences in community assembly mechanisms, with model fit (R^2) ranging from 24.6% in Minjiang estuary to 75.7% in Pingtan. Moreover, stochastic processes played a more important role in shaping aloricate communities, whereas deterministic processes dominated in tintinnids. These findings demonstrate regional-scale differences in ciliate distribution patterns and assembly mechanisms during spring, providing insights into ecological assessment and management of nearshore ecosystems in southeastern China.

Keyword: planktonic ciliate; aloricate ciliate and tintinnid; distribution pattern; community assembly; southeastern China

1 INTRODUCTION

Investigating the assembly mechanisms of microeukaryotic communities and their responses to environmental and spatial factors is a central topic in ecology, as it is crucial for understanding the processes that maintain ecosystem functioning and for predicting ecosystem responses to external driving forces (Hanson et al., 2012; Chen et al., 2017; Kong et al., 2019). As a major group of microeukaryotes, ciliates play a crucial role in energy flow and biogeochemical cycling within marine ecosystems (Azam et al., 1983; Landry and Calbet, 2004; Calbet and Saiz, 2005). Furthermore, their high sensitivity to environmental changes makes them ideal bioindicators for monitoring ecosystem health (Kato and Taniguchi, 1993; Xu et al., 2011; Jiang et al., 2013b; Sun et al., 2017; Wang et al., 2021b).

* Supported by the National Natural Science Foundation of China (Nos. 42176147, 42141003) and the Xiamen Key Laboratory of Urban Sea Ecological Conservation and Restoration (USER)

** Corresponding author: zhangwenjing@xmu.edu.cn

In recent years, an increasing number of studies have demonstrated that the structure of planktonic the structure of planktonic ciliate communities is jointly shaped by both environmental and spatial factors, with the relative importance of these factors varying considerably across ecosystem types and study scale (Pan et al., 2020; Liu et al., 2021a; Xu et al., 2022). For instance, in intertidal sandy beaches, Pan et al. (2020) reported that environmental variables such as temperature, salinity, and nutrients, together with spatial factors like geographic distance, jointly influenced the spatial distribution of ciliates, with environmental factors exerting slightly stronger effects. Similarly, Liu et al. (2021a) found that the taxonomic composition of ciliate communities was primarily driven by environmental conditions in the South China Sea intertidal waters, whereas spatial gradients from neritic to oceanic water areas played a more significant role in shaping the spatial heterogeneity of community structure. Marine planktonic ciliates are classified into loricate and aloricate groups, which differ in ecological strategies, trophic modes, and habitat preferences, potentially leading to distinct responses to environmental and spatial variability (Gómez, 2007; Lynn, 2008; Wang et al., 2023a). For example, loricate ciliates (e.g., tintinnids) exhibited higher abundance and biomass at coastal stations in the northern Yellow Sea near Zhangzi Island, while aloricate ciliates dominated offshore sites, with their abundance positively correlated with chlorophyll-*a* (Chl-*a*) concentration (Yu et al., 2013). In addition to horizontal gradients, vertical gradients represent an important spatial scale influencing the distribution of ciliate communities (Grattepanche et al., 2016; Hu et al., 2016; Santoferrara et al., 2018). As demonstrated by a study conducted in the Western Pacific, ciliate communities exhibited distinct vertical distribution, with elevated diversity observed at the deep chlorophyll maximum and 200-m layer (Zhao et al., 2017). These findings highlight the complex interplay between environmental and spatial factors in shaping ciliate diversity across diverse marine environments, providing critical insights into ecosystem dynamics and informing conservation and management strategies. However, how these factors interact through deterministic and stochastic processes to govern community assembly remains a core challenge in microbial ecology.

To understand whether environmental and spatial factors drive communities through deterministic or stochastic processes, we turn to two competing ecological theories. The niche-based theory posits that community assembly is primarily governed by deterministic processes, including abiotic environmental factors and biotic interactions (Chesson, 2000; Fargione et al., 2003). In contrast, the neutral theory suggests that microbial communities are predominantly shaped by stochastic processes such as birth, death, colonization, extinction, and speciation (Chave, 2004; Sloan et al., 2006; Zhou and Ning, 2017). Recent studies have demonstrated that the relative importance of stochastic and deterministic processes varies depending on ecosystem type, spatial scale, and environmental gradients (Sun et al., 2020; Mo et al., 2021; Jiao et al., 2022; Yu et al., 2022; Lian et al., 2023; Li et al., 2024). For instance, Yu et al. (2022) investigated ciliate communities in the Ross Sea, Antarctica, and found that the contribution of stochastic processes to ciliate communities depended on spatial location, being lower in offshore areas compared to nearshore and transitional areas. Lian et al. (2023) demonstrated that microbial community assembly in the East China Sea exhibited a clear depth-dependent pattern, with stochastic processes predominating in surface waters, while their influence diminishes with increasing depth, accompanied by a strengthened role of deterministic processes. Moreover, anthropogenic perturbations are also recognized as important factors influencing microbial community structure (Ager et al., 2010; Ning et al., 2024; Niu et al., 2024). In coastal areas of the Bohai and Yellow seas that were heavily impacted by human activities, deterministic processes played a dominant role in shaping protistan communities (Qiao et al., 2024). Additionally, existing research has predominantly focused on loricate ciliates, which are generally more sensitive to abiotic factors such as temperature, salinity, eutrophication, and pollution (Jiang et al., 2013a; Liang et al., 2018; Li et al., 2023), implying that their community structure is possibly more strongly governed by deterministic processes. However, region-specific studies on the community assembly mechanisms of planktonic ciliates in the nearshore waters of southeastern China remain limited, particularly with respect to systematic comparisons between loricate and aloricate ciliates.

The nearshore waters of southeastern China, located in the subtropical marine monsoon zone, is characterized by a highly convoluted shoreline with numerous bays and estuaries. This region is shaped by multiple anthropogenic disturbances—including urbanization, industrial and agricultural pollution, and

climate change—as well as complex hydrodynamic forces such as the Zhe-Min Coastal Current (ZMCC), the South China Sea Warm Current (SCSWC), and the South China Sea Branch of the Kuroshio Current (SCSBK), forming a highly dynamic and complex nearshore ecosystem (Yang et al., 2004; Halpern et al., 2008; Yang et al., 2008; Belkin, 2009; Guo et al., 2019; Xu et al., 2020). The coupling of distinctive natural conditions and intensive anthropogenic activities makes this region an ideal "natural laboratory" for investigating ciliate distribution and community assembly.

In this study, we investigated the ciliate community composition and its relationship with environmental and spatial factors across 578 samples from five representative regions in the nearshore waters of southeastern China, using high-throughput sequencing targeting the V4 region of the 18S rRNA gene. The main objectives were to: (1) elucidate the community composition and spatial distribution patterns of planktonic ciliates in the study area; (2) identify the key environmental drivers shaping the community structure of aloricate ciliates and tintinnids; and (3) evaluate the relative roles of neutral processes and environmental selection to community assembly across different regions and ciliate morphological groups.

2 MATERIAL AND METHOD

2.1 Study area, sampling and physico-chemical analysis

From 18 to 28 May 2020, five scientific research vessels were deployed for synchronous surveys across five representative regions in the nearshore waters of southeastern China. From south (23.614 9°N, 117.538 3°E) to north (26.726 2°N, 119.742 7°E), the study covered: Dongshan Bay (DS), Xiamen Bay (XM), Pingtan region (PT), Minjiang estuary (MJ), and Sansha Bay (SS) (Fig.1), spanning approximately 3 752 km of coastline. Specifically, Dongshan Bay and Sansha Bay serve as key aquaculture zones in China, where long-term intensive mariculture activities have had profound impacts on the marine environment (Chen et al., 2014, 2019; Wang et al., 2023b; Luo et al., 2024). The Minjiang River, the largest river in Fujian Province, delivers substantial inputs of organic matter and nutrients to its estuarine region, which serves as a key spawning ground for a variety of economically important fish species (Liu et al., 2022a). Xiamen Bay, a typical semi-enclosed harbor, is particularly affected by multiple anthropogenic disturbances, including port construction, shipping activities, and pollutant inputs from the Jiulong River (Chen et al., 2013; Hu et al., 2019; Wu et al., 2021). In contrast, the nearshore waters near Pingtan Island experience relatively low human disturbance and are primarily influenced by open-ocean currents. Both surface water (0.5–2 m) and bottom water (5–72 m) were collected in 14 to 28 sampling stations in each sea area. The collected water samples were initially pre-filtered through a sieve with a 200-μm aperture to eliminate meso- and macroplankton, debris, and sediment. Subsequently, 300–1 000 mL of pre-filtered water was filtered through a 3-μm polycarbonate membrane filter (47-mm diameter, Millipore). The membrane filters were stored at -80 °C until DNA extraction.

Water temperature, salinity, and depth were measured in situ using conductivity-temperature-depth (CTD) oceanic profilers. Additional chemical parameters, including nitrite (NO_2^-), nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), silicate (SiO_3^{2-}), and Chl *a*, were also measured following standard methods (Dick and Tabatabai, 1977; Welschmeyer, 1994; Pai et al., 2001; Dai et al., 2008; Yan et al., 2012). Detailed sample information and the measured environmental variables are provided in Supplementary Table S1.

2.2 DNA extraction, PCR, and sequencing

We extracted total genomic DNA using DNA Clean & ConcentratorTM-25 kit (Zymo Research, Irvine, CA, USA). The hypervariable V4 region (270 – 387 base pairs, bp) of the 18S rRNA gene was amplified using the primers TAReuk454FWD1 (5′-CCAGCA(G/C)C(C/T)GCGGTAATTCC-3′) and TAReukREV3 (5′-ACTTTCGTTCTTGAT(C/T)(A/G)A-3′) (Stoeck et al., 2006). PCR amplification was performed with an initial denaturation at 94 °C for 3 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 30 s. A final extension step was carried out at 72 °C for 5 min. The resulting PCR products were purified using the Cycle Pure Kit (Omega Bio-tek, Norcross, GA, USA) and subsequently utilized for library construction, followed by quality control and paired-end 250-bp sequencing on the Illumina NovaSeq 6000 platform.

2.3 Sequence analysis

Raw sequencing reads were initially filtered

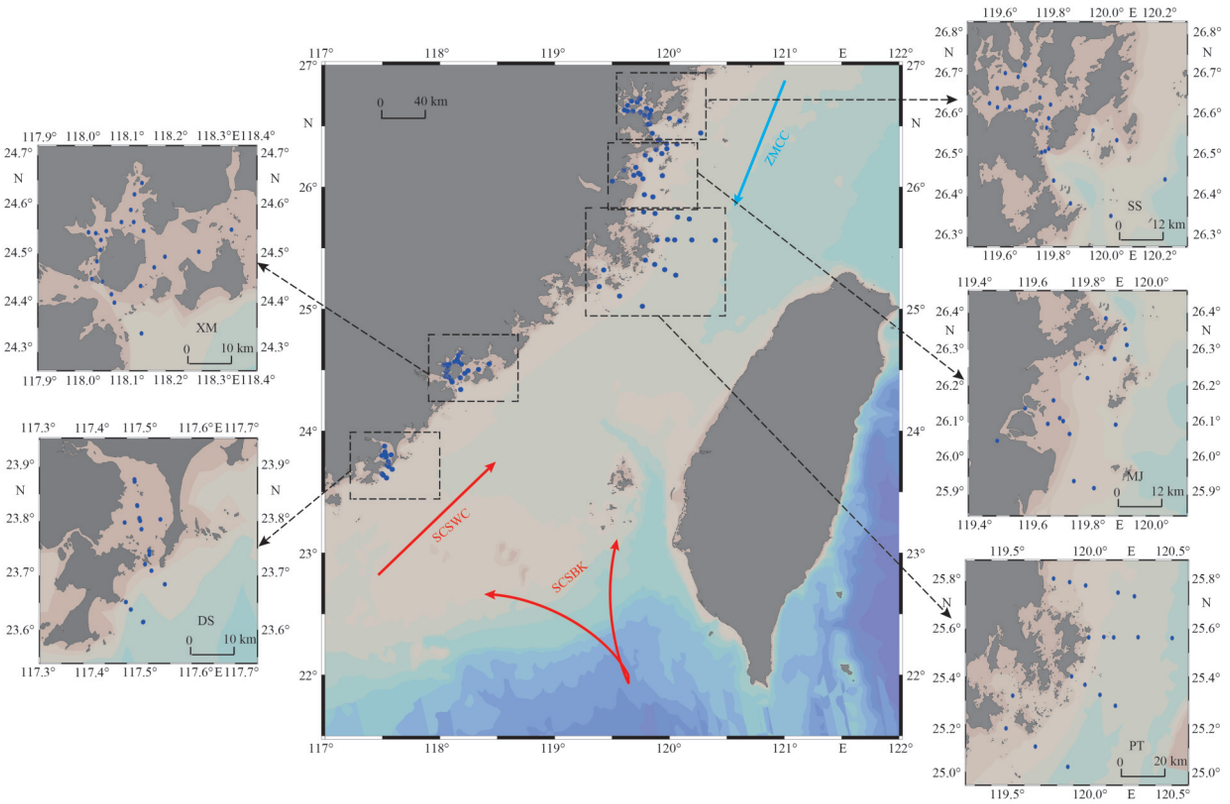


Fig.1 Circulation patterns in the Taiwan Strait in spring 2020 and sampling regions in the nearshore waters of southeastern China

DS: Dongshan Bay; XM: Xiamen Bay; PT: Pingtan region; MJ: Minjiang estuary; SS: Sansha Bay; SCSWC: South China Sea Warm Current; ZMCC: Zhe-Min Coastal Current; SCSBK: South China Sea Branch of the Kuroshio Current.

using Trimmomatic v0.33 (Bolger et al., 2014) to eliminate low-quality bases, followed by adaptor and primer trimming with Cutadapt (Martin, 2011) (v1.9.1). The retained high-quality sequences were subsequently assembled using USEARCH v10 (Edgar, 2013), and chimeric sequences were identified and removed using UCHIME v8.1 (Edgar et al., 2011). Sequence denoising was performed with the DADA2 algorithm (Callahan et al., 2016) implemented in QIIME 2 (v2020.06) (Bolyen et al., 2019), resulting in the generation of amplicon sequence variants (ASVs). Taxonomic annotation was conducted based on the Protist Ribosomal Reference (PR2) Database (v4.14.1) (Guillou et al., 2013) employing an 80% confidence threshold for classification. After manually removing all non-ciliate ASVs, the resulting ciliate-only ASV table was used for subsequent analyses.

2.4 Morphological classification of ciliates

Ciliates were classified into two groups—loricate and aloricate—based on the presence or absence of a lorica structure. Trait information was primarily obtained from published literature (Lynn, 2008; Adl et al., 2019). For taxa with unclear classification, trait assignments were inferred from congeneric species or higher taxonomic levels when necessary.

2.5 Statistical analysis

The map of sampling stations in nearshore waters of southeastern China was drawn by Ocean Data View (ODV, version 5.6.7) (R. Schlitzer, Ocean Data View, 2003, http://www. awi-bremerhaven.de/GEO/ODV). To comprehensively characterize the spatial patterns, environmental drivers and underlying assembly processes of ciliate communities, we applied a multi-step analytical framework including diversity assessment, multivariate ordination, environmental association analyses, and community assembly inference. Alpha diversity indices, including Shannon, ACE, and Pielou indices, were calculated in R (v4.3.2) environment using the "vegan" package to characterize within-sample diversity patterns and community evenness across different regions. Analysis of variance (ANOVA) was conducted using SPSS V26.0 to test the

significance of diversity indices and environmental parameters across different regions, with results visualized through box plots presenting different lettering indicates significant differences (post-hoc Tukey test). Additionally, linear associations between diversity indices and environmental parameters were generated using Pearson's correlation model, with *P*-values adjusted for multiple comparisons using the Benjamini-Hochberg FDR procedure (α= 0.05). Beta-diversity was assessed using the Bray-Curtis dissimilarity index and visualized through non-metric multidimensional scaling (NMDS) to visualize variations in ciliate community composition among samples and groups. Significant difference (P<0.05) between groups was assessed by analysis of similarities (ANOSIM). The Mantel test, redundancy analysis (RDA), and canonical correspondence analysis (CCA) implemented in the "vegan" package were used to assess the strength and structure of associations between environmental variables and ciliate community composition (Diniz-Filho et al., 2013), with Mantel test *P*-values adjusted by the Benjamini-Hochberg FDR procedure (α=0.05) to account for multiple comparisons. Moreover, the "rdacca. hp" package was applied to quantify the independent contributions of individual environmental factors to community variation (Liu et al., 2023). Variation partitioning analysis (VPA) was performed to quantify the relative importance of spatial variables and environmental variables in assembly. Environmental variables were transformed using a [log(1+x)] function (x represents the original value) and those with variance inflation factors (VIF) greater than 20 were removed to reduce multicollinearity while retaining ecologically interpretable predictors (Lepš and Šmilauer, 1999; Mo et al., 2018). The remaining variables were subjected to forward selection (P<0.05) (Blanchet et al., 2008). Spatial factors were represented by a set of spatial eigenfunction variables derived from principal coordinates of neighbour matrices (PCNM). PCNM variables were generated based on the geographic configuration of sampling sites (i.e., inter-station distances calculated from station latitude-longitude coordinates) and treated as candidate spatial predictors. These variables were then screened using forward selection (P<0.05), and the retained PCNM variables were included in subsequent analyses together with environmental factors (Griffith and Peres-Neto, 2006). Spearman correlations (R) were calculated among ASVs with a relative abundance greater than 0.01% using the "WGCNA" and "psych" packages. Co-occurrence network analysis was performed to explore the potential associations among ciliate ASVs and to characterize network structure and stability. In the network analysis, only correlations with *P*-values< 0.05 and $|r|$>0.6 were retained (Barberán et al., 2012; Liu and Jiang, 2020; Zhang et al., 2021). Network visualization was completed by Gephi version 0.10.1 (Bastian et al., 2009). To assess network structural stability, robustness was evaluated by randomly removing 50% of the nodes, while the maximum node vulnerability value within the network was used as an indicator of network fragility (Yuan et al., 2021). Niche breadth was estimated using the "niche. width" function in the R package "spaa". In addition, the Sloan neutral community model (NCM) was constructed using the "Hmisc", "minpack. lm" and "stats4" packages in R to assess the potential importance of stochastic processes in ciliate communities (Sloan et al., 2006). The parameter Nm in the model represents the estimate of species migration between communities, while the R^2 determines the overall fit to the NCM (Pan et al., 2020).

3 RESULT

3.1 Spatial hydrological structure

This study systematically investigated the spatial variation of environmental factors across five representative regions along the nearshore waters of southeastern China (Fig.2; one-way ANOVA results in Supplementary Table S2): (a) temperature was significantly higher in XM than in the other regions, followed by DS, with the lowest values recorded in SS; (b) salinity exhibited the greatest range of variation in the MJ, likely due to the influence of freshwater inputs (e.g., rivers) and tidal activity in the estuarine area; salinity in PT and DS was significantly higher than in the other regions, while the XM showed the lowest salinity; (c) ammonium and phosphate concentrations were significantly higher in XM and SS compared to the other three regions, and both showed high spatial variability; (d) nitrate and nitrite were significantly higher in MJ, SS, and XM than in the other regions; (e) silicate was highest in MJ, with the greatest variability also observed in this region; (f) all nutrient parameters measured in PT were consistently at the lowest levels among the five regions; (g) no significant differences in Chl *a* were observed across the five regions.

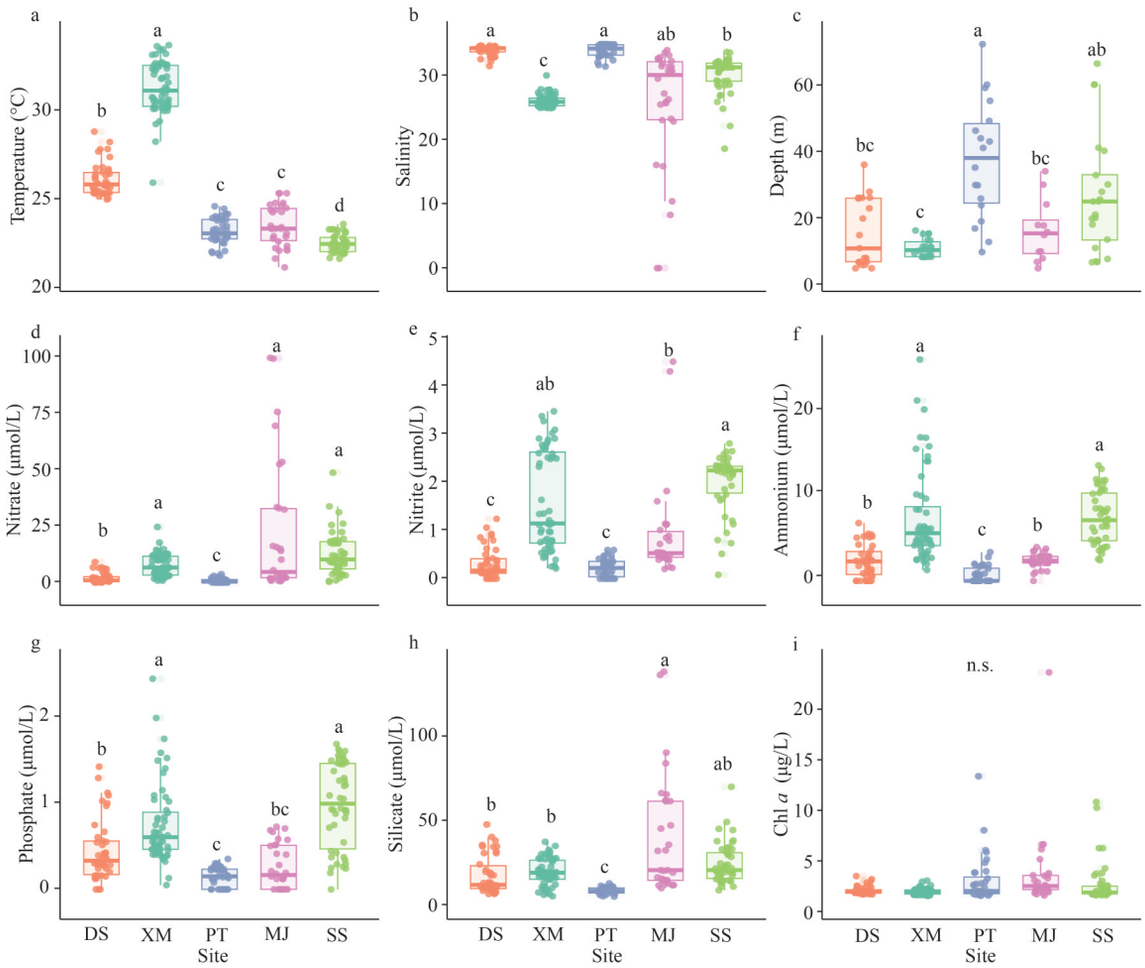


Fig.2 Boxplots showing the spatial variation of environmental parameters across five regions in the nearshore waters of southeastern China

Variables include temperature (a), salinity (b), depth (c), nitrate (d), nitrite (e), ammonium (f), phosphate (g), silicate (h), and chlorophyll *a* (Chl *a*) (i). Letters above boxes indicate significant differences among regions based on post-hoc comparisons (Tukey's HSD test, $P<0.001$); groups sharing a letter are not significantly different. n.s.: non-significant differences.

3.2 Ciliate community composition and alpha diversity

A total of 770 707 high-quality ciliate reads and 140 ciliate ASVs were retrieved from all samples. These ASVs were assigned to 6 classes that originated from 21 families and 36 genera. The 6 classes were Spirotrichea, Oligohymenophorea, Prostomatea, Litostomatea, Phyllopharyngea, and Colpodea. Among them, 95 ASVs were identified as aloricate ciliates and 30 as tintinnids (class Spirotrichea), representing 80.7% and 11.4% of the total ciliate reads, respectively. Venn diagram results showed that 62 aloricate ciliate ASVs (65%) were present in all five regions, whereas only 16 tintinnid ASVs (53%) were shared across the five regions (Fig.3a).

At the class level, Spirotrichea consistently exhibited higher relative abundance than other ciliate classes across all regions, making it the dominant class in the study area (Fig.4b). Notably, in the PT, Oligohymenophorea and Colpodea showed greater relative abundance compared to the other regions, indicating a regional advantage in abundance. At the genus level, *Spirotontonia* was dominant in the MJ and SS, whereas *Unclassified-Strombidiidae* showed higher relative abundance in the DS and XM (Fig.4b).

Ciliate community diversity indices revealed that both the ACE and Shannon indices were significantly higher in the DS compared to the other regions ($P<0.001$), while the lowest diversity values were observed in the MJ and PT (Fig.4a). A decreasing trend in alpha diversity was observed

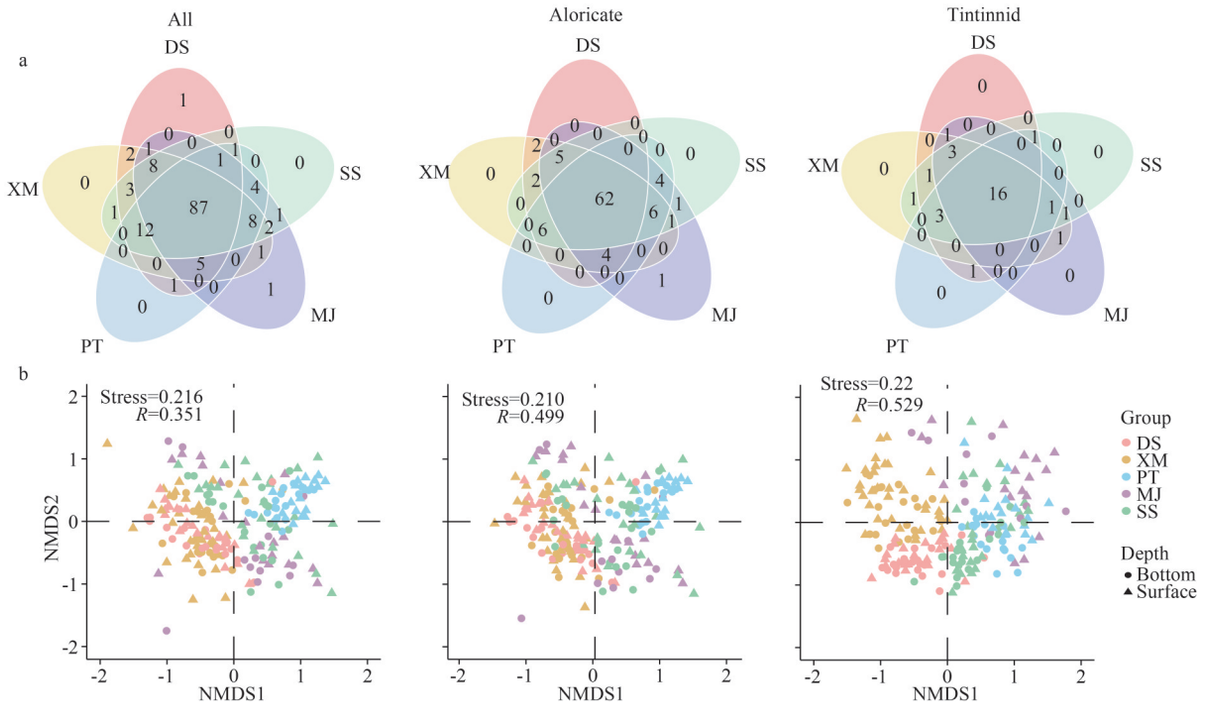


Fig.3 Compositional differences of planktonic ciliate communities across five southeastern regions among distinct morphological groups

a. Venn diagram showing the number of aloricate, tintinnid and total ASVs in the five regions; b. non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis community similarity.

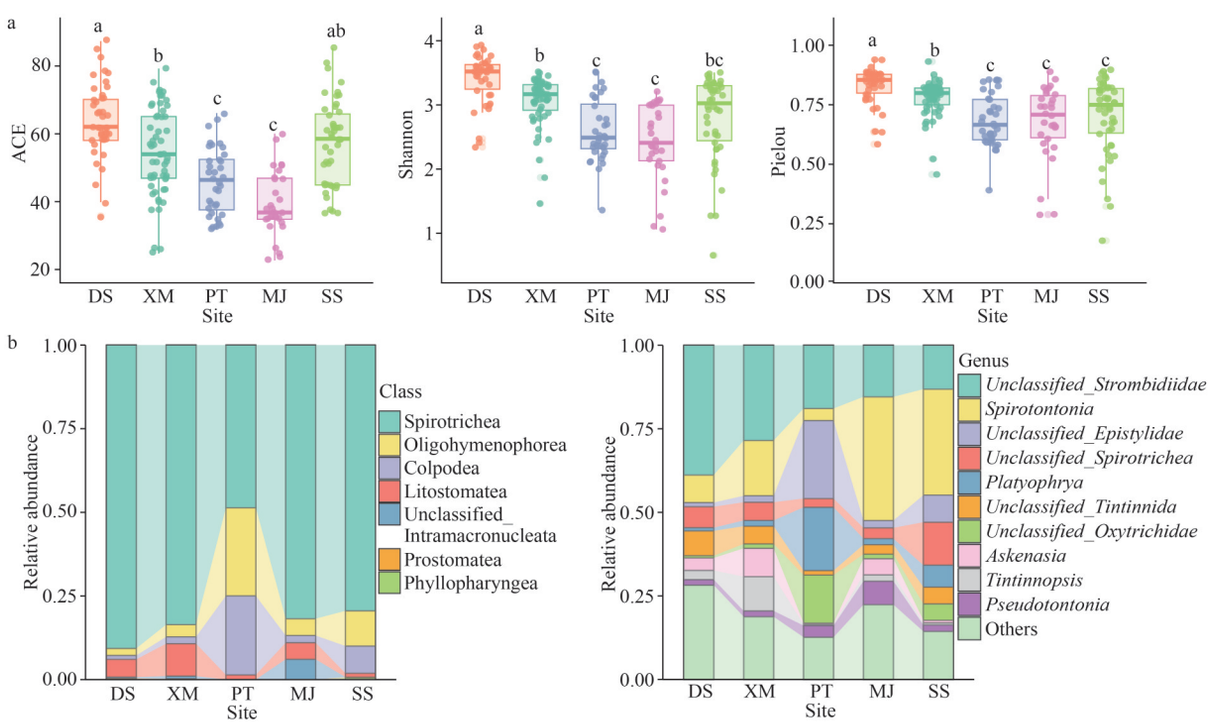


Fig.4 Alpha diversity and taxonomic composition of ciliate communities across five regions

a. comparison of alpha diversity indices of ciliate communities across five regions. Each point represents a sample, and box boundaries indicate the interquartile range with the median shown as a horizontal line. Letters above boxes indicate significant differences among regions based on post-hoc comparisons (Tukey's HSD test, $P<0.001$); b. relative abundance of ciliate communities at the class (left) and genus (right) levels across the five regions.

from south to north, spanning from DS to MJ. However, the ACE index in the northernmost region, SS, was significantly higher than in PT and MJ (P<0.001). The Pielou index in DS and XM was also significantly greater than that in the remaining regions (P<0.001).

Pearson correlation analysis between ciliates' diversity and environmental parameters revealed that (1) temperature, salinity, depth, phosphate, and nitrite were positively correlated with diversity indices (P<0.05); (2) Chl *a*, nitrate, and silicate were negatively correlated; (3) diversity indices were significantly negatively correlated with both latitude and longitude (Supplementary Fig.S1).

3.3 Relationship between environmental factors, spatial factors, and planktonic ciliates

Based on Bray-Curtis dissimilarity, the NMDS results revealed significant spatial differentiation of ciliate communities across the southeastern Chinese coastal waters (ANOSIM, P=0.001). Tintinnids showed the greatest spatial separation (ANOSIM, R=0.529, P=0.001), followed by aloricate ciliates (ANOSIM, R=0.499, P=0.001) and the total ciliate community (ANOSIM, R=0.351, P=0.001) (Fig.3b).

RDA and CCA, together with hierarchical partitioning analysis (rdacca.hp), indicated that temperature was the most influential environmental factor affecting planktonic ciliate communities, regardless of loricate or aloricate forms, particularly for tintinnids, explaining 31.17% of the community variation (P<0.05), followed by salinity (14.44%) and phosphate (11.08%) (Fig.5a). Mantel tests further supported the above findings and revealed a strong correlation between community structure and Chl *a* (P<0.01) (Fig.5b & Supplementary Table S3). Additionally, phosphate showed the highest correlation with community composition in the DS and SS, while ammonium was most strongly associated with communities in PT. In MJ, nitrate and salinity exhibited the strongest correlations, potentially reflecting estuarine input. Salinity also showed the highest correlation with community structure in XM (Fig.5b & Supplementary Table S4). Notably, depth had no significant effect on community structure in most regions or on either aloricate ciliates or tintinnids, except in DS.

Variance partitioning analysis (VPA) quantified the relative contributions of environmental and spatial factors to variations in ciliate community structure (Fig.6 & Supplementary Table S5). At the regional scale, pure environmental variables dominated community composition in DS, PT, and MJ, with explained variances ranging from 0.13 to 0.19, suggesting the important role of environmental selection in community assembly. In contrast, pure spatial variables dominated community composition in SS, indicating that dispersal limitation may play a key role in the region. At the morphological group level, pure environmental variables dominated community composition in both aloricate ciliates and tintinnids, explaining 10% and 11% of the variation, respectively. Overall, pure environmental factors accounted for a larger proportion of the explained variance than pure spatial factors along the southeastern coast. Additionally, a high proportion of unexplained variance (0.57–0.76) was observed across both regions and morphological groups.

3.4 Complexity and stability of co-occurrence networks in the nearshore waters of southeastern China

To evaluate the complexity and stability of planktonic ciliate communities across the nearshore waters of southeastern China, co-occurrence networks were constructed based on ASV relative abundance (Fig.7). Correlation and topological properties of each network are summarized in Table 1. The network correlation results showed that the DS, XM, PT, MJ, and SS networks consisted of 81, 62, 47, 82, and 76 nodes, respectively, with corresponding edge numbers of 433, 126, 146, 203, and 319. Across all regional networks, the proportion of positive correlations exceeded that of negative correlations. MJ exhibited the highest proportion of positive edges (94.58%), while DS had the lowest (68.59%), indicating stronger synergistic interactions within the MJ ciliate community. Overall, the proportion of positive correlations followed the order: MJ>SS>XM>PT> DS.

In terms of network complexity, the DS network exhibited the highest complexity, characterized by the largest number of connections and the highest average degree (10.691), followed by SS. In contrast, XM and PT networks showed relatively low complexity. The SS network showed the highest average clustering coefficient (0.677), which may reflect stronger local synergies and potential functional coordination among ciliate taxa. The XM network had the highest modularity (0.611), followed by MJ (0.595), indicating relatively partitioned network structures in these regions.

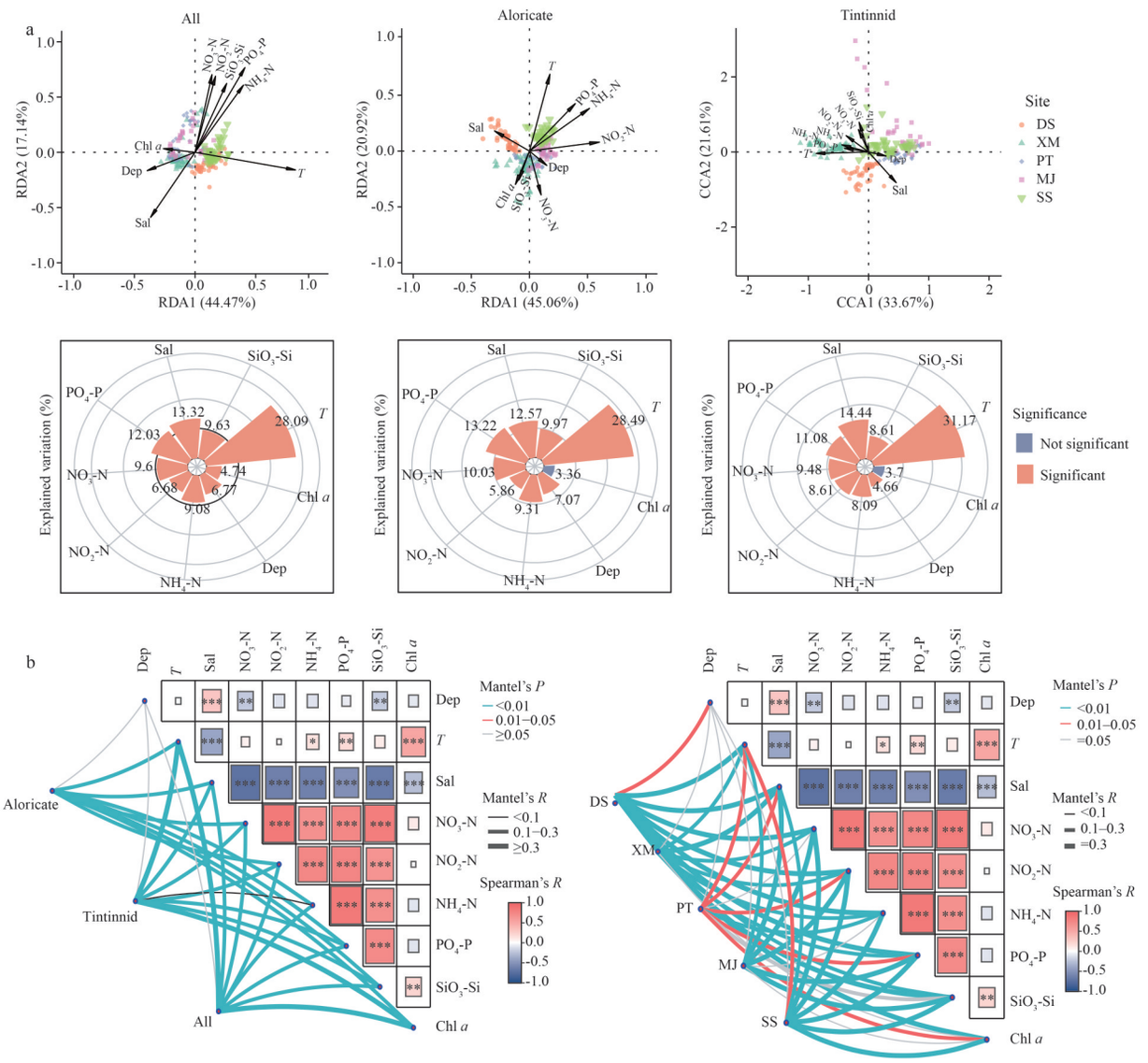


Fig.5 Relationships between planktonic ciliate communities and environmental factors in the nearshore waters of southeastern China

a. RDA and CCA illustrate the influence of environmental variables on overall, aloricate, and loricate (tintinnid) ciliate communities. Radar plots below show the independent contributions of each variable, with significance indicated by color; b. Mantel and Spearman correlation analyses reveal associations between environmental factors and ciliate communities (left) and sampling regions (right). Line colors indicate Mantel's *P* values (cyan, $P<0.01$; red, $0.01 \le P < 0.05$; gray, $P \ge 0.05$), and asterisks indicate the significance levels of Spearman correlations (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$).

possibly influenced by stronger environmental selection within the community. The PT network exhibited the highest network density (0.135) and the shortest average path length (1.558), suggesting greater transmission efficiency.

In terms of network stability, the SS exhibited the highest robustness under random removal of 50% of the nodes, reflecting strong resistance to stochastic node loss. The robustness of the other networks ranked as DS>XM>MJ>PT (Fig.7b). In contrast, with respect to network vulnerability, the MJ network exhibited the highest vulnerability, followed by the PT, whereas the DS network showed the lowest vulnerability (Fig.7c). Overall, DS and SS exhibited higher network structural stability, whereas MJ and PT showed lower structural stability.

The overall network complexity was low, with an average degree of 3.86 and a network density of 0.055. However, the network exhibited a relatively high average clustering coefficient (0.682) and modularity index (0.689), indicating the presence of



Fig.6 Variation partitioning analysis (VPA) showing the relative contributions of environmental and spatial factors to ciliate community composition across five regions and between tintinnid and aloricate ciliate groups

Analyses were performed separately for each region and trait-based group. Asterisks indicate significance levels: *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$.

localized synergistic structures and functional compartmentalization within the network. In addition, the network showed the highest vulnerability and a moderate level of robustness, reflecting its relatively low stability under external disturbances.

3.5 Community assembly mechanisms of ciliate communities

The NCM results indicated significant regional differences in the extent to which community assembly was influenced by stochastic processes (Fig.8a), with the R^2 ranked as follows: PT (0.757)> DS (0.549)>SS (0.487)>XM (0.452)>MJ (0.246). Among these, PT exhibited the highest R^2 (0.757) and migration rate (m=0.02165), suggesting that its community structure was predominantly shaped by stochastic processes with frequent species dispersal. In contrast, MJ showed the lowest R^2 (0.246) and migration rate (m=0.01536), implying a relatively weak role of stochasticity, likely due to limited species exchange. Furthermore, ciliate communities in DS and XM exhibited significantly greater niche breadth than those in the other three regions, among which no significant differences were observed (Fig.8b).

In addition to spatial variation, community assembly processes also differed between morphological groups. Aloricate ciliates showed a better fit to the neutral model (R^2=0.431), indicating

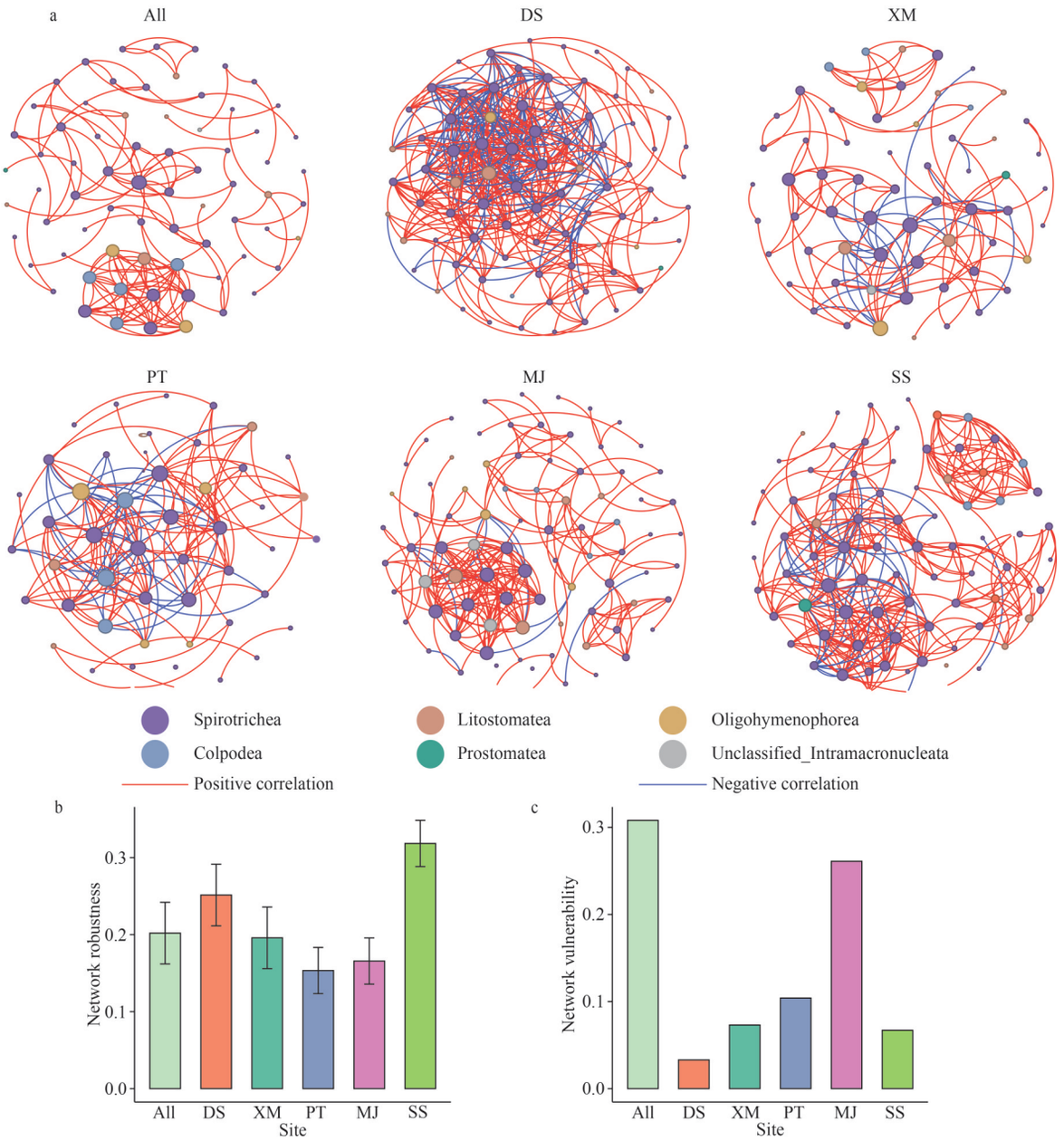


Fig.7 Co-occurrence network analysis and stability metrics of ciliate communities across five regions and all sites

a. class-level co-occurrence network analysis; b. robustness was measured as the proportion of taxa that remained after 50% of the taxa were randomly removed from each network; c. network vulnerability measured by maximum node vulnerability in each network.

Table 1 Correlations and topological properties of co-occurrence networks of ciliate communities in different regions

Network topological indicator	All	DS	XM	MJ	PT	SS
Node	71	81	62	82	47	76
Edge	137	433	126	203	146	319
Proportion of positive correlation	1.000	0.686	0.794	0.946	0.712	0.856
Average degree	3.859	10.691	4.065	4.951	6.213	8.395
Average path length	1.792	1.739	2.276	3.174	1.558	1.627
Network density	0.055	0.134	0.067	0.061	0.135	0.112
Average clustering coefficient	0.682	0.545	0.512	0.628	0.654	0.677
Modularity	0.689	0.331	0.611	0.595	0.378	0.524

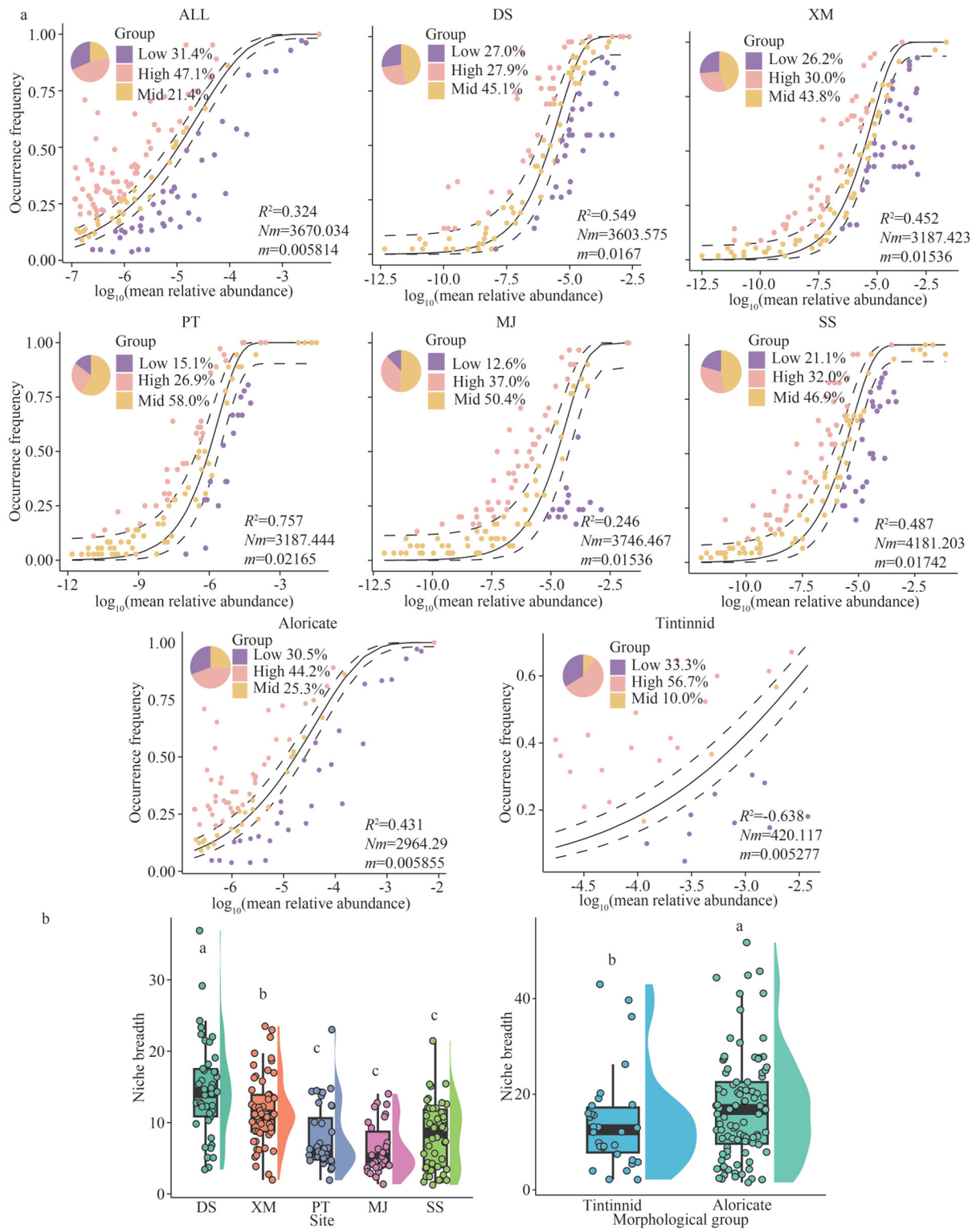


Fig.8 Neutral community model fitting and niche breadth comparisons of planktonic ciliates across regions and morphological groups

a. neutral community model (NCM) fitting for all sites (ALL), five coastal regions, and two morphological groups. The solid black line indicates the best fit to the NCM, and dashed lines represent the 95% confidence intervals. ASVs occurring more or less frequently than predicted by the NCM are shown in pink ("high") and purple ("low"), respectively, while those within the prediction range are shown in yellow ("mid"). Pie charts represent the proportion of ASVs in each category; b. comparison of niche breadth among regions (left) and between tintinnid and aloricate ciliate groups (right). Different letters denote significant differences (P<0.05).

stochastic processes played a more prominent role in shaping aloricate communities. In contrast, tintinnids showed a negative neutral model fit (R^2= -0.638), indicating a marked departure from neutral expectations and suggesting deterministic environmental filtering may play a more important role in their assembly. Additionally, aloricate ciliates exhibited significantly wider niche breadths than tintinnids (Fig.8b).

4 DISCUSSION

4.1 Diversity pattern and composition of planktonic ciliates in the nearshore waters of southeastern China

This study systematically analyzed the diversity patterns and composition of planktonic ciliate communities across five regions along the nearshore waters of southeastern China. In terms of community composition, Spirotrichea was identified as the dominant class across all regions, consistent with previous findings on marine planktonic ciliates reported in the Shenzhen estuary, Laizhou Bay, Taiwan Strait, and the western Pacific (Sun et al., 2020; Jiang et al., 2021; Li et al., 2022; Wan et al., 2024). Furthermore, the study by Gao et al. (2009) corroborated the representative taxa of Spirotrichea in Chinese coastal waters, highlighting its broad distribution and ecological predominance in coastal ecosystems. Notably, our study found that aloricate ciliates dominated the communities in the nearshore waters of southeastern China, consistent with patterns observed in other subtropical nearshore ecosystems (Martínez-López et al., 2019; Sun et al., 2019). The relative abundance of Oligohymenophorea and Colpodea in PT was significantly higher than those in other regions, indicating that PT may provide more suitable ecological niches for these ciliate groups, thereby promoting their environmental adaptation and population reproduction. Previous studies have demonstrated that the distribution of Oligohymenophorea is closely associated with seawater depth, with its members tending to inhabit deeper waters (Zhao and Xu, 2016; Santoferrara et al., 2023). Wan et al. (2024) further reported an increasing trend in both the proportion and sequence abundance of parasitic taxa such as Oligohymenophorea and Colpodea with depth, based on vertical profiling of ciliate communities from surface to deep waters in the western Pacific. Notably, Oligohymenophorea exhibited the most distinct vertical community differentiation across the entire water column. PT is characterized by a greater average water depth compared to bay regions (e.g., DS, XM, SS) and estuarine region (e.g., MJ) (Fig.2c), a hydrological feature that may contribute to the favorable conditions supporting the survival of Oligohymenophorea and Colpodea. Our study revealed significant differences in the dominant genera across various marine regions, with the genus *Spirotontonia* exhibiting the highest relative abundance in the MJ and SS. As aloricate ciliates, their rapid growth, short generation times, and fast population turnover may enable them to respond more strongly to nutrient enrichment and other environmental changes (Pierce and Turner, 1992). Previous studies have demonstrated that both MJ and SS are representative eutrophic zones; however, they differ substantially in nutrient sources and hydrodynamic conditions. The MJ is strongly influenced by the runoff from the Minjiang River, transporting large amounts of allochthonous nutrients and resulting in persistent high-nutrient conditions (Zheng, 2010; Wang et al., 2020a; Yang, 2020). In contrast, SS is a subtropical semi-enclosed bay connected to the East China Sea via a narrow outlet, which limits water exchange. Long-term intensive aquaculture activities have further exacerbated nutrient accumulation in this region, leading to sustained eutrophic conditions (Sun et al., 2015; Wang et al., 2020b; Xie et al., 2020; Zhu et al., 2022). In coastal regions characterized by high nutrient and intensive mariculture—such as Baisha Bay and Dapeng Cove in the South China Sea—*Spirotontonia* is frequently reported as a dominant genus within the planktonic ciliate community, particularly in spring (Wu et al., 2016, 2017).

Interestingly, we observed a gradually decreasing trend in the diversity indices of planktonic ciliates from the DS to the MJ in the nearshore waters of southeastern China (Fig.4a). This diversity pattern was highly consistent with the findings of Gu et al. (2024), who reported a significant increase in microbial plankton diversity with decreasing latitude along a subtropical coastal gradient, illustrating a typical latitudinal diversity gradient. The formation of such latitudinal diversity patterns is generally driven by multiple environmental factors, among which temperature is considered one of the key drivers (Hillebrand, 2004; Mittelbach et al., 2007). On the one hand, elevated temperatures can accelerate organismal metabolism and growth rates, thereby promoting ecological differentiation and

enhancing species diversity (Brown et al., 2004; Allen et al., 2006; Yvon-Durocher and Allen, 2012; Brodie and Mannion, 2023). On the other hand, higher temperatures facilitate nutrient uptake and assimilation by phytoplankton, promote biomass accumulation, stimulating their growth and subsequently providing sufficient food resources for planktonic ciliates (Gillooly et al., 2001; Rose and Caron, 2007; Cross et al., 2015). Meanwhile, our results revealed a significant positive correlation between diversity indices and temperature, and a significant negative correlation with spatial factors (P<0.05), further supporting the above findings. Furthermore, other environmental factors, such as salinity and nutrient levels, may also influence ciliate diversity to varying degrees.

However, the high diversity observed in the SS was an exception. This result may be attributed to the high phosphate levels in this region. Previous studies have shown that phosphorus is one of the limiting nutrients for bacterial and phytoplankton growth, and increased phosphorus availability has been shown to significantly enhance bacterial biomass accumulation and stimulate phytoplankton growth, thereby providing a more abundant food source for ciliates (Taylor, 1986; Lomas et al., 2014; Paczkowska et al., 2019). Moreover, our results revealed a significant positive correlation between phosphate and the diversity indices (P<0.001) (Supplementary Fig.S1).

4.2 Response of planktonic ciliate community distribution within the nearshore waters of southeastern China to environmental and spatial factors

In this study, temperature was identified as the primary environmental driver influencing the community structure of planktonic ciliates along the nearshore waters of southeastern China, consistently influencing both tintinnids and aloricate ciliate communities. This result was consistent with previous findings on microeukaryotes (Liu et al., 2021b; Gu et al., 2024). Previous studies have demonstrated that temperature can influence species richness, metabolic activity, and the relative abundance of specific taxa in planktonic ciliates, thereby modulating energy flow and niche distribution, and ultimately increasing spatial heterogeneity in their communities (Norf and Weitere, 2010; Vidussi et al., 2011; Domaizon et al., 2012). Notably, the ecological impacts of temperature are not unidirectional or uniformly positive, but instead involve complex regulatory mechanisms. For instance, high temperature fluctuations can alter the protistan community composition, resulting in declines or even local extinctions of certain taxa, while increasing community heterogeneity (Zander et al., 2017). In contrast, low temperatures often reduce the metabolic rates and reproductive success of protists, while selectively constraining the activity and distribution of specific functional groups, thereby enhancing community-level spatial heterogeneity (Rose and Caron, 2007; Rose et al., 2009).

Further analyses revealed that both environmental and spatial variables significantly influenced ciliate community structure, with their relative importance varying across regions (Fig.6). In SS, for instance, the pure spatial variables explained a larger proportion of community variation than the pure environmental variables, suggesting a predominant role of spatial processes in this region. This pattern is likely related to the complex and enclosed geomorphological and hydrodynamic features of SS. Previous studies have reported that Sansha Bay is characterized by dense island distributions and intricate current systems, where terrain-driven tidal flows generate numerous microscale semi-enclosed water masses (Lin et al., 2017, 2018; Wang et al., 2019a). These conditions limit water exchange and microbial dispersal, thereby intensifying the role of dispersal limitation. Similar patterns have been observed in other microbial communities (Ma et al., 2021, 2023; Zhu et al., 2022). For example, Ma et al. (2021) reported that spatial variables based on geographic distance explained a greater proportion of variation in microeukaryotes than environmental factors in Sansha Bay. Likewise, Zhu et al. (2022) found a similar spatial driven pattern in bacterial communities within the same region, further supporting spatial processes may play a dominant role in the formation of community heterogeneity in enclosed bays with limited hydrological connectivity. However, in DS, PT, and MJ, environmental variables have a more significant impact on the ciliate community structure, which may be related to regional ecogeographic features, such as intense local hydrodynamic disturbances or anthropogenic activities (Gu et al., 2020; Zou, 2022; Shao et al., 2023). For example, Shao et al. (2023) demonstrated that salinity, nitrite, and phosphate significantly shaped microeukaryotic communities in the MJ. These environmental fluctuations were closely linked to shellfish aquaculture activities and hydrodynamic conditions near river mouths, which

in turn weakened the role of spatial processes in community assembly. Additionally, the effects of tides and ocean currents should not be overlooked (Zhang et al., 2015; Sun et al., 2020; Kalu et al., 2023). The SCSWC and SCSBK can introduce warm, oligotrophic waters from the open ocean into nearshore areas, which may dilute local nutrient concentrations and influence ciliate community structure. In contrast, the ZMCC delivers nutrient-enriched waters from coastal runoff and river discharges, and may be associated with higher ciliate diversity and biomass in the affected areas. Notably, VPA results revealed a considerable proportion of unexplained variation across regions, ranging from 0.57 to 0.76 (Fig.6). This unexplained variation might come from the combined effects of biotic interactions, methodological limitations, unmeasured environmental factors, and stochastic processes (Hanson et al., 2012; Stegen et al., 2013; Lima-Mendez et al., 2015; Wei et al., 2016). Biotic interactions (e.g., predation, competition, and parasitism) can strongly structure microbial communities but are rarely quantified in situ and thus are difficult to incorporate into statistical models (Faust and Raes, 2012; Lima-Mendez et al., 2015). In addition, unmeasured environmental factors, such as resource-field structure (bacterial and phytoplankton community composition) and organic matter content, have been shown to significantly shape microbial and protistan distribution patterns (Rehman et al., 2025; Wen et al., 2025). Methodologically, variation partitioning is based on linear ordination and regression frameworks and may fail to capture threshold effects, nonlinear responses, or interactions among processes, which can lead to underestimation of the explainable component (Smith and Lundholm, 2010). Finally, stochastic processes (ecological drift) are pervasive in microbial communities and can contribute substantial unexplained variation even along strong environmental gradients (Zhou and Ning, 2017).

Finally, we found that depth had no significant impact on the distribution of ciliates in most regions or on either loricate or aloricate ciliates (Supplementary Tables S3 & S4). This result was consistent with the findings of studies on the planktonic ciliate community structure in the Beibu Gulf (Wang et al., 2014). Nevertheless, studies in the Taiwan Strait, East China Sea, and western Pacific have demonstrated that depth plays a crucial role in ciliate community structure (Zhao et al., 2017; Sun et al., 2020; Wang et al., 2021a). This discrepancy may be attributed to the vertically well-mixed water columns in the southeastern nearshore areas, which limits water column stratification and thereby reduces the effect of depth gradients on the vertical distribution of ciliates.

4.3 Regional difference in planktonic ciliate co-occurrence networks and their assembly mechanisms

Microbial interactions are a significant factor shaping the community structure. There, co-occurrence networks, have been widely applied in different ecosystems (including soil, reservoirs, oceans, and polar regions) to study the potential interactions among microorganisms, providing a critical foundation for evaluating the complexity and stability of microbial communities (Barberán et al., 2012; He et al., 2017; Li et al., 2021; Yu et al., 2023). Our research found that network structural stability was relatively high in SS and DS, whereas MJ and PT exhibited lower structural stability (Fig.7). Several explanations may account for the result. Firstly, compared to MJ and PT, SS and DS exhibited higher levels of biodiversity. Previous studies have demonstrated that greater species diversity enhances the functional redundancy and response capacity of ecosystems, thereby improving the resistance of biological communities to environmental disturbances (Pennekamp et al., 2018; Wu et al., 2025). This was also consistent with the diversity-stability theory (Wang et al., 2019b). Secondly, as a typical estuarine area, MJ was frequently subjected to multiple influences such as freshwater input, nutrient fluctuations, and human activities, leading to frequent shifts in microbial community structure and thereby reducing community stability (Yi et al., 2020; Suzzi et al., 2022; Zhou et al., 2023). Additionally, we found that MJ and PT exhibit higher network vulnerability, indicating that the network may be more dependent on key species in these regions, and once key species are lost, network stability rapidly declines (Philippot et al., 2021; Kajihara and Hynson, 2024).

Our NCM results revealed significant regional differences in the contribution of stochastic processes to ciliate community assembly. Specifically, PT exhibited the highest contribution, while DS, SS, and XM showed intermediate levels, and MJ exhibited the lowest (Fig.8a). This significant spatial heterogeneity may be closely related to the hydrodynamic characteristics,

topographic structure, human activities, and nutrient levels across regions. PT is a typical open nearshore water area, significantly influenced by hydrodynamic disturbances such as offshore tides, coastal currents, and wind-driven waves. These factors enhance water mixing and species dispersal, thereby promoting the dominance of stochastic processes in community assembly (Xiao et al., 2002; Pan et al., 2013; Zhu, 2013). Meanwhile, PT exhibited relatively low variability in environmental factors and low nutrient levels, resulting in weaker pressure in environmental selection. DS, SS, and XM are characterized by relatively enclosed bay environments and weaker hydrodynamic conditions compared to PT, which limit species dispersal and migration, thereby reducing the influence of stochastic processes in community assembly. In particular, DS and SS are typical aquaculture zones where long-term intensive mariculture activities have led to nutrient accumulation, which in turn enhances the role of environmental selection to some extent (Zheng, 2019; Pan et al., 2021; Zhu et al., 2022; Ma et al., 2023). As a typical harbor region, XM is subject to long-term disturbances from urbanization, port activities, and pollutant inputs from the Jiulong River, which may limit the stochastic dispersal of some species and strengthen environmental selection (Wu et al., 2021; Yan et al., 2024). Estuarine regions are shaped by freshwater runoff and terrestrial inputs, creating strong environmental gradients and nutrient fluctuations that enhance environmental selection (Lin et al., 2024; Wu et al., 2025). Similar patterns in human-impacted estuaries such as the Zhujiang (Pearl) and Changjiang (Yangtze) rivers support the link between environmental disturbance intensity and community assembly processes (Liu et al., 2022b; Xian et al., 2024).

Notably, the neutral model results showed a better fit for aloricate ciliates, whereas tintinnids exhibited a strongly negative fit (R^2=-0.638), indicating a marked departure from neutral expectations and providing strong evidence that deterministic environmental filtering dominates tintinnid community assembly. This divergence may be attributed to differences in their niche breadths. Previous studies have indicated that deterministic processes tend to exert stronger influences on communities with narrower niche widths, while their effects are comparatively weaker on communities with broader niches (Pandit et al., 2009; Wu et al., 2018). However, the NCM cannot fully explain the community assembly process, indicating the involvement of non-neutral mechanisms such as environmental filtering and species interactions (Mo et al., 2021; Yu et al., 2022). These findings highlight the need for future studies to further explore the interplay between stochasticity, determinism, and functional traits in shaping microbial community assembly, which will also provide important insights for understanding biodiversity patterns and informing conservation strategies in dynamic marine ecosystems.

5 CONCLUSION

This study investigated spring diversity patterns and community composition of planktonic ciliates in five representative regions in the nearshore waters of southeastern China, as well as their responses to environmental and spatial factors. The results revealed significant spatial variation in ciliate community composition. Spirotrichea was the dominant class across all regions, with aloricate ciliates prevailing throughout the study area. Environmental variables played a dominant role in shaping communities in the DS, PT, and MJ, whereas spatial factors exerted a stronger influence in SS. Network analysis indicated higher structural stability in the DS and SS, suggesting that communities in these regions were more resistant to external disturbances, in contrast to the MJ and PT. Furthermore, the NCM revealed significant differences in community assembly mechanisms across regions and morphological groups of ciliates, with stochastic processes playing significant roles in shaping aloricate ciliate communities, while tintinnids were primarily structured by deterministic processes. Nevertheless, this study has certain limitations. For instance, sampling was restricted to the spatial scales, lacking seasonal or interannual data, which may underestimate the temporal dynamics of ciliate communities. Future research should incorporate long-term time-series monitoring and integrate multi-omics approaches such as metagenomics to systematically investigate the spatiotemporal succession and functional drivers of ciliate communities. Overall, this study will provide a foundation for a deeper understanding of their assembly processes and dynamic responses, and offer theoretical support for the protection and management of nearshore ecosystems.

6 DATA AVAILABILITY STATEMENT

All 18S rRNA gene sequence data from this study have been submitted to the NCBI database (www.ncbi.nlm.nih.gov/) under accession No. SRP466473 and BioProject accession No. PRJNA1028181.

7 ACKNOWLEDGMENT

The authors thank Senjie LIN, Ling LI, Yujie WANG, Jiashun LI, Sitong LIN, Huatao YUAN, Chengmin ZHU, Yifan MA, Qianqian LIU from Xiamen University for their assistance with sampling collection.

References

Adl S M, Bass D, Lane C E et al. 2019. Revisions to the classification, nomenclature, and diversity of eukaryotes. *Journal of Eukaryotic Microbiology*, **66**(1): 4-119, https://doi.org/10.1111/jeu.12691.

Ager D, Evans S, Li H et al. 2010. Anthropogenic disturbance affects the structure of bacterial communities. *Environmental Microbiology*, **12**(3): 670-678, https://doi.org/10.1111/j.1462-2920.2009.02107.x.

Allen A P, Gillooly J F, Savage V M et al. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences of the United States of America*, **103**(24): 9130-9135, https://doi.org/10.1073/pnas.0603587103.

Azam F, Fenchel T, Field J G, et al. 1983. The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, **10**(3): 257-263, https://doi.org/10.3354/meps010257.

Barberán A, Bates S T, Casamayor E O et al. 2012. Using network analysis to explore co-occurrence patterns in soil microbial communities. *The ISME Journal*, **6**(2): 343-351, https://doi.org/10.1038/ismej.2011.119.

Bastian M, Heymann S, Jacomy M. 2009. Gephi: an open source software for exploring and manipulating networks. *Proceedings of the International AAAI Conference on Web and Social Media*, **3**(1): 361-362, https://doi.org/10.1609/icwsm.v3i1.13937.

Belkin I M. 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography*, **81**(1-4): 207-213, https://doi.org/10.1016/j.pocean.2009.04.011.

Blanchet F G, Legendre P, Borcard D. 2008. Forward selection of explanatory variables. *Ecology*, **89**(9): 2623-2632, https://doi.org/10.1890/07-0986.1.

Bolger A M, Lohse M, Usadel B. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*, **30**(15): 2114-2120, https://doi.org/10.1093/bioinformatics/btu170.

Bolyen E, Rideout J R, Dillon M R et al. 2019. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, **37**(8): 852-857, https://doi.org/10.1038/s41587-019-0209-9.

Brodie J F, Mannion P D. 2023. The hierarchy of factors predicting the latitudinal diversity gradient. *Trends in Ecology & Evolution*, **38**(1): 15-23, https://doi.org/10.1016/j.tree.2022.07.013.

Brown J H, Gillooly J F, Allen A P et al. 2004. Toward a metabolic theory of ecology. *Ecology*, **85**(7): 1771-1789, https://doi.org/10.1890/03-9000.

Calbet A, Saiz E. 2005. The ciliate-copepod link in marine ecosystems. *Aquatic Microbial Ecology*, **38**(2): 157-167, https://doi.org/10.3354/ame038157.

Callahan B J, McMurdie P J, Rosen M J et al. 2016. DADA2: high-resolution sample inference from Illumina amplicon data. *Nature Methods*, **13**(7): 581-583, https://doi.org/10.1038/nmeth.3869.

Chave J. 2004. Neutral theory and community ecology. *Ecology Letters*, **7**(3): 241-253 https://doi.org/10.1111/j.1461-0248.2003.00566.x.

Chen B H, Ji W D, Chen J M et al. 2013. Characteristics of nutrients in the Jiulong River and its impact on Xiamen Water, China. *Chinese Journal of Oceanology and Limnology*, **31**(5): 1055-1063, https://doi.org/10.1007/s00343-013-2263-3.

Chen B H, Ji W D, Zhou K W et al. 2014. Nutrient and eutrophication characteristics of the Dongshan Bay, South China. *Chinese Journal of Oceanology and Limnology*, **32**(4): 886-898, https://doi.org/10.1007/s00343-014-3214-3.

Chen W D, Pan Y B, Yu L Y et al. 2017. Patterns and processes in marine microeukaryotic community biogeography from Xiamen coastal waters and intertidal sediments, Southeast China. *Frontiers in Microbiology*, **8**: 1912, https://doi.org/10.3389/fmicb.2017.01912.

Chen Y Z, Wang Y S, Xie T T et al. 2019. Analysis for the change of aquaculture area and water quality in Sansha Bay during 2010-2018. *In*: IGARSS 2019-2019 IEEE International Geoscience and Remote Sensing Symposium. IEEE, Yokohama, Japan. p.8264-8267, https://doi.org/10.1109/IGARSS.2019.8897917.

Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology*, *Evolution*, *and Systematics*, **31**(1): 343-366, https://doi.org/10.1146/annurev.ecolsys.31.1.343.

Cross W F, Hood J M, Benstead J P et al. 2015. Interactions between temperature and nutrients across levels of ecological organization. *Global Change Biology*, **21**(3): 1025-1040, https://doi.org/10.1111/gcb.12809.

Dai M H, Wang L F, Guo X H et al. 2008. Nitrification and inorganic nitrogen distribution in a large perturbed river/estuarine system: the Pearl River estuary, China. *Biogeosciences*, **5**(9): 1227-1244, https://doi.org/10.5194/bg-5-1227-2008.

Dick W A, Tabatabai M A. 1977. Determination of orthophosphate in aqueous solutions containing labile organic and inorganic phosphorus compounds. *Journal of Environmental Quality*, **6**(1): 82-85, https://doi.org/10.2134/jeq1977.00472425000600010018x.

Diniz-Filho J A F, Soares T N, Lima J S et al. 2013. Mantel test in population genetics. *Genetics and Molecular*

Biology, **36**(4): 475-485, https://doi.org/10.1590/S1415-47572013000400002.

Domaizon I, Lepère C, Debroas D et al. 2012. Short-term responses of unicellular planktonic eukaryotes to increases in temperature and UVB radiation. *BMC Microbiology*, **12**(1): 202, https://doi.org/10.1186/1471-2180-12-202.

Edgar R C. 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nature Methods*, **10**(10): 996-998, https://doi.org/10.1038/nmeth.2604.

Edgar R C, Haas B J, Clemente J C et al. 2011. UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics*, **27**(16): 2194-2200, https://doi.org/10.1093/bioinformatics/btr381.

Fargione J, Brown C S, Tilman D. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America*, **100**(15): 8916-8920, https://doi.org/10.1073/pnas.1033107100.

Faust K, Raes J. 2012. Microbial interactions: from networks to models. *Nature Reviews Microbiology*, **10**(8): 538-550, https://doi.org/10.1038/nrmicro2832.

Gómez F. 2007. Trends on the distribution of ciliates in the open Pacific Ocean. *Acta Oecologica*, **32**(2): 188-202, https://doi.org/10.1016/j.actao.2007.04.002.

Gao S, Gong J, Lynn D et al. 2009. An updated phylogeny of oligotrich and choreotrich ciliates (Protozoa, Ciliophora, Spirotrichea) with representative taxa collected from Chinese coastal waters. *Systematics and Biodiversity*, **7**(2): 235-242, https://doi.org/10.1017/S1477200009002989.

Gillooly J F, Brown J H, West G B et al. 2001. Effects of size and temperature on metabolic rate. *Science*, **293**(5538): 2248-2251, https://doi.org/10.1126/science.1061967.

Grattepanche J D, Santoferrara L F, McManus G B et al. 2016. Unexpected biodiversity of ciliates in marine samples from below the photic zone. *Molecular Ecology*, **25**(16): 3987-4000, https://doi.org/10.1111/mec.13745.

Griffith D A, Peres-Neto P R. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology*, **87**(10): 2603-2613, https://doi.org/10.1890/0012-9658(2006)87[2603:SMIETF]2.0.CO;2.

Gu R, Sun P, Wang Y et al. 2020. Genetic diversity, community assembly, and shaping factors of benthic microbial eukaryotes in Dongshan Bay, Southeast China. *Frontiers in Microbiology*, **11**: 592489, https://doi.org/10.3389/fmicb.2020.592489.

Gu Y F, Lin S J, Mo Y Y et al. 2024. Niche features and assembly mechanisms of microeukaryotic generalists and specialists along a north-south gradient of a subtropical coastal sea. *Marine Ecology Progress Series*, **742**: 35-57, https://doi.org/10.3354/meps14647.

Guillou L, Bachar D, Audic S et al. 2013. The Protist Ribosomal Reference database (PR2): a catalog of unicellular eukaryote Small Sub-Unit rRNA sequences with curated taxonomy. *Nucleic Acids Research*, **41**(D1): D597-D604, https://doi.org/10.1093/nar/gks1160.

Guo J S, Zhang Z X, Xia C S et al. 2019. Seasonal characteristics and forcing mechanisms of the surface Kuroshio branch intrusion into the South China Sea. *Acta Oceanologica Sinica*, **38**(1): 13-21, https://doi.org/10.1007/s13131-017-1132-x.

Halpern B S, Walbridge S, Selkoe K A et al. 2008. A global map of human impact on marine ecosystems. *Science*, **319**(5865): 948-952, https://doi.org/10.1126/science.1149345.

Hanson C A, Fuhrman J A, Horner-Devine M C et al. 2012. Beyond biogeographic patterns: processes shaping the microbial landscape. *Nature Reviews Microbiology*, **10**(7): 497-506, https://doi.org/10.1038/nrmicro2795.

He S B, Guo L X, Niu M Y et al. 2017. Ecological diversity and co-occurrence patterns of bacterial community through soil profile in response to long-term switchgrass cultivation. *Scientific Reports*, **7**(1): 3608, https://doi.org/10.1038/s41598-017-03778-7.

Hillebrand H. 2004. On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**(2): 192-211, https://doi.org/10.1086/381004.

Hu S K, Campbell V, Connell P et al. 2016. Protistan diversity and activity inferred from RNA and DNA at a coastal ocean site in the eastern North Pacific. *FEMS Microbiology Ecology*, **92**(6): fiw050, https://doi.org/10.1093/femsec/fiw050.

Hu W J, Yu W W, Ma Z Y et al. 2019. Assessing the ecological sensitivity of coastal marine ecosystems: a case study in Xiamen Bay, China. *Sustainability*, **11**(22): 6372, https://doi.org/10.3390/su11226372.

Jiang C Q, Liu B, Zhang J et al. 2021. Diversity and seasonality dynamics of ciliate communities in four estuaries of Shenzhen, China (South China Sea). *Journal of Marine Science and Engineering*, **9**(3): 260, https://doi.org/10.3390/jmse9030260.

Jiang Y, Xu H L, Hu X Z et al. 2013a. Functional groups of marine ciliated protozoa and their relationships to water quality. *Environmental Science and Pollution Research*, **20**(8): 5272-5280, https://doi.org/10.1007/s11356-013-1525-0.

Jiang Y, Yang E J, Min J O et al. 2013b. Using pelagic ciliated microzooplankton communities as an indicator for monitoring environmental condition under impact of summer sea-ice reduction in western Arctic Ocean. *Ecological Indicators*, **34**: 380-390, https://doi.org/10.1016/j.ecolind.2013.05.026.

Jiao S, Chu H Y, Zhang B G et al. 2022. Linking soil fungi to bacterial community assembly in arid ecosystems. *iMeta*, **1**(1): e2, https://doi.org/10.1002/imt2.2.

Kajihara K T, Hynson N A. 2024. Networks as tools for defining emergent properties of microbiomes and their stability. *Microbiome*, **12**(1): 184, https://doi.org/10.1186/s40168-024-01868-z.

Kalu E I, Reyes-Prieto A, Barbeau M A. 2023. Community dynamics of microbial eukaryotes in intertidal mudflats in the hypertidal bay of Fundy. *ISME Communications*, **3**(1): 21, https://doi.org/10.1038/s43705-023-00226-8.

Kato S, Taniguchi A. 1993. Tintinnid ciliates as indicator species of different water masses in the western North Pacific Polar Front. *Fisheries Oceanography*, **2**(3-4): 166-174, https://doi.org/10.1111/j.1365-2419.1993.tb00132.x.

Kong J, Wang Y, Warren A et al. 2019. Diversity distribution and assembly mechanisms of planktonic and benthic microeukaryote communities in intertidal zones of southeast Fujian, China. *Frontiers in Microbiology*, **10**: 2640, https://doi.org/10.3389/fmicb.2019.02640.

Landry M R, Calbet A. 2004. Microzooplankton production in the oceans. *ICES Journal of Marine Science*, **61**(4): 501-507, https://doi.org/10.1016/j.icesjms.2004.03.011.

Lepš J, Šmilauer P. 1999. Multivariate Analysis of Ecological Data. Faculty of Biological Sciences, University of South Bohemia, České Budějovice.

Li H B, Wang C F, Zhao L et al. 2023. Variability of tintinnid ciliate communities with water masses in the western Pacific Ocean. *Journal of Plankton Research*, **45**(3): 509-522, https://doi.org/10.1093/plankt/fbad011.

Li S Z, Yan X, Abdullah Al M et al. 2024. Ecological and evolutionary processes involved in shaping microbial habitat generalists and specialists in urban park ecosystems. *mSystems*, **9**(6): e00469-24, https://doi.org/10.1128/msystems.00469-24.

Li W L, Xu D P, Ji D D. 2022. Community composition and seasonal variation of planktonic ciliates in Sanshan Island, Laizhou Bay. *Oceanologia et Limnologia Sinica*, **53**(6): 1441-1454, https://doi.org/10.11693/hyhz20220400113. (in Chinese with English abstract)

Li X, Wan W J, Zheng L X et al. 2021. Community assembly mechanisms and co-occurrence patterns of nitrite-oxidizing bacteria communities in saline soils. *Science of the Total Environment*, **772**: 145472, https://doi.org/10.1016/j.scitotenv.2021.145472.

Lian K Y, Liu F L, Li Y et al. 2023. Environmental gradients shape microbiome assembly and stability in the East China sea. *Environmental Research*, **238**: 117197, https://doi.org/10.1016/j.envres.2023.117197.

Liang C, Li H B, Dong Y et al. 2018. Planktonic ciliates in different water masses in open waters near Prydz Bay (East Antarctica) during austral summer, with an emphasis on tintinnid assemblages. *Polar Biology*, **41**(11): 2355-2371, https://doi.org/10.1007/s00300-018-2375-5.

Lima-Mendez G, Faust K, Henry N et al. 2015. Determinants of community structure in the global plankton interactome. *Science*, **348**(6237): 1262073, https://doi.org/10.1126/science.1262073.

Lin H Y, Hu J Y, Zhu J et al. 2017. Tide- and wind-driven variability of water level in Sansha Bay, Fujian, China. *Frontiers of Earth Science*, **11**(2): 332-346, https://doi.org/10.1007/s11707-016-0588-x.

Lin J W, You Y X, Liu G X. 2018. Numerical research of the tidal currents in Sansha Bay. *Journal of Fisheries Research*, **40**(6): 413-424, https://doi.org/10.14012/j.cnki.fjsc.2018.06.001. (in Chinese with English abstract)

Lin L, Xiong J Z Q, Liu L H et al. 2024. Microbial interactions strengthen deterministic processes during community assembly in a subtropical estuary. *Science of the Total Environment*, **906**: 167499, https://doi.org/10.1016/j.scitotenv.2023.167499.

Liu Q, Jiang Y. 2020. Application of microbial network analysis to discriminate environmental heterogeneity in Fildes Peninsula, Antarctica. *Marine Pollution Bulletin*, **156**: 111244, https://doi.org/10.1016/j.marpolbul.2020.111244.

Liu W W, McManus G B, Lin X F et al. 2021a. Distribution patterns of ciliate diversity in the South China Sea. *Frontiers in Microbiology*, **12**: 689688, https://doi.org/10.3389/fmicb.2021.689688.

Liu X P, Xie N D, Bai M H et al. 2021b. Composition change and decreased diversity of microbial eukaryotes in the coastal upwelling waters of South China Sea. *Science of the Total Environment*, **795**: 148892, https://doi.org/10.1016/j.scitotenv.2021.148892.

Liu Y, Ma C, Zhao W W et al. 2022a. Research on characteristics of community structure of fish in Minjiang estuary and adjacent waters in spring and summer. *Journal of Fisheries Research*, **44**(5): 467-476, https://doi.org/10.14012/j.cnki.fjsc.2022.05.005. (in Chinese with English abstract)

Liu Y, Yu X, Yu Y et al. 2023. Application of "rdacca.hp" R package in ecological data analysis: case and progress. *Chinese Journal of Plant Ecology*, **47**(1): 134-144, https://doi.org/10.17521/cjpe.2022.0314. (in Chinese with English abstract)

Liu Z B, Wei Q Y, Zou D Y et al. 2022b. Deterministic factors determine the comammox community composition in the Pearl River estuary Ecosystem. *Microbiology Spectrum*, **10**(4): e01016-22, https://doi.org/10.1128/spectrum.01016-22.

Lomas M W, Bonachela J A, Levin S A et al. 2014. Impact of ocean phytoplankton diversity on phosphate uptake. *Proceedings of the National Academy of Sciences of the United States of America*, **111**(49): 17540-17545, https://doi.org/10.1073/pnas.1420760111.

Luo J, Wang N, Zhu Y J et al. 2024. Seasonal effects of fish, seaweed and abalone cultures on dissolved organic matter and carbon sequestration potential in Sansha Bay, China. *Science of the Total Environment*, **945**: 174144, https://doi.org/10.1016/j.scitotenv.2024.174144.

Lynn D H. 2008. The Ciliated Protozoa: Characterization, Classification, and Guide to the Literature. 3rd edn. Springer Netherlands, Dordrecht.

Ma Y F, Huang L F, Zhang W J. 2023. Environment drives the co-occurrence of bacteria and microeukaryotes in a typical subtropical bay. *Journal of Oceanology and Limnology*, **41**(6): 2292-2308, https://doi.org/10.1007/s00343-022-2268-x.

Ma Y F, Pan Y B, Liu Q Q et al. 2021. Co-occurrence patterns and assembly processes of microeukaryotic communities in a semi-enclosed aquaculture bay. *Continental Shelf Research*, **228**: 104550, https://doi.org/10.1016/j.csr.2021.104550.

Martínez-López A, Pérez-Morales A, Ayala-Rodríguez G A et al. 2019. Abundance and seasonal variability of aloricate ciliates and tintinnids in a eutrophic coastal lagoon system of the Gulf of California, Mexico. *Regional Studies in Marine Science*, **32**: 100814, https://doi.org/10.1016/j.rsma.2019.100814.

Martin M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet Journal*, **17**(1): 10-12, https://doi.org/10.14806/ej.17.1.200.

Mittelbach G G, Schemske D W, Cornell H V et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**(4): 315-331, https://doi.org/10.1111/j.1461-0248.2007.01020.x.

Mo Y Y, Peng F, Gao X F et al. 2021. Low shifts in salinity determined assembly processes and network stability of microeukaryotic plankton communities in a subtropical urban reservoir. *Microbiome*, **9**(1): 128, https://doi.org/10.1186/s40168-021-01079-w.

Mo Y Y, Zhang W J, Yang J et al. 2018. Biogeographic patterns of abundant and rare bacterioplankton in three subtropical bays resulting from selective and neutral processes. *The ISME Journal*, **12**(9): 2198-2210, https://doi.org/10.1038/s41396-018-0153-6.

Ning D L, Wang Y J, Fan Y P et al. 2024. Environmental stress mediates groundwater microbial community assembly. *Nature Microbiology*, **9**(2): 490-501, https://doi.org/10.1038/s41564-023-01573-x.

Niu X F, Wang H, Wang T et al. 2024. The combination of multiple environmental stressors strongly alters microbial community assembly in aquatic ecosystems. *Journal of Environmental Management*, **350**: 119594, https://doi.org/10.1016/j.jenvman.2023.119594.

Norf H, Weitere M. 2010. Resource quantity and seasonal background alter warming effects on communities of biofilm ciliates. *FEMS Microbiology Ecology*, **74**(2): 361-370, https://doi.org/10.1111/j.1574-6941.2010.00948.x.

Paczkowska J, Rowe O F, Figueroa D et al. 2019. Drivers of phytoplankton production and community structure in nutrient-poor estuaries receiving terrestrial organic inflow. *Marine Environmental Research*, **151**: 104778, https://doi.org/10.1016/j.marenvres.2019.104778.

Pai S C, Tsau Y J, Yang T I. 2001. pH and buffering capacity problems involved in the determination of ammonia in saline water using the indophenol blue spectrophotometric method. *Analytica Chimica Acta*, **434**(2): 209-216, https://doi.org/10.1016/S0003-2670(01)00851-0.

Pan A J, Wan X F, Guo X G et al. 2013. Responses of the Zhe-Min coastal current adjacent to Pingtan Island to the wintertime monsoon relaxation in 2006 and its mechanism. *Science China Earth Sciences*, **56**(3): 386-396, https://doi.org/10.1007/s11430-012-4429-9.

Pan Y B, Yang J, McManus G B et al. 2020. Insights into protist diversity and biogeography in intertidal sediments sampled across a range of spatial scales. *Limnology and Oceanography*, **65**(5): 1103-1115, https://doi.org/10.1002/lno.11375.

Pan Z, Liu Q L, Jiang R G et al. 2021. Microplastic pollution and ecological risk assessment in an estuarine environment: the Dongshan Bay of China. *Chemosphere*, **262**: 127876, https://doi.org/10.1016/j.chemosphere.2020.127876.

Pandit S N, Kolasa J, Cottenie K. 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology*, **90**(8): 2253-2262, https://doi.org/10.1890/08-0851.1.

Pennekamp F, Pontarp M, Tabi A et al. 2018. Biodiversity increases and decreases ecosystem stability. *Nature*, **563**(7729): 109-112, https://doi.org/10.1038/s41586-018-0627-8.

Philippot L, Griffiths B S, Langenheder S. 2021. Microbial community resilience across ecosystems and multiple disturbances. *Microbiology and Molecular Biology Reviews*, **85**(2): e00026-20, https://doi.org/10.1128/mmbr.00026-20.

Pierce R W, Turner J T. 1992. Ecology of planktonic ciliates in marine food webs. *Reviews in Aquatic Sciences*, **6**(2): 139-181.

Qiao W W, Li H B, Zhang J Y et al. 2024. Comparing the environmental influences and community assembly of protist communities in two anthropogenic coastal areas. *Microorganisms*, **12**(8): 1618, https://doi.org/10.3390/microorganisms12081618.

Rehman A, Wang J, Yue H et al. 2025. Algal organic matter alters protistan community structure and assembly processes in coastal sediments. *European Journal of Protistology*, **97**: 126134, https://doi.org/10.1016/j.ejop.2025.126134.

Rose J M, Caron D A. 2007. Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. *Limnology and Oceanography*, **52**(2): 886-895, https://doi.org/10.4319/lo.2007.52.2.0886.

Rose J M, Vora N M, Countway P D et al. 2009. Effects of temperature on growth rate and gross growth efficiency of an Antarctic bacterivorous protist. *The ISME Journal*, **3**(2): 252-260, https://doi.org/10.1038/ismej.2008.96.

Santoferrara L F, Qureshi A, Sher A et al. 2023. The photic-aphotic divide is a strong ecological and evolutionary force determining the distribution of ciliates (Alveolata, Ciliophora) in the ocean. *Journal of Eukaryotic Microbiology*, **70**(5): e12976, https://doi.org/10.1111/jeu.12976.

Santoferrara L F, Rubin E, Mcmanus G B. 2018. Global and local DNA (meta)barcoding reveal new biogeography patterns in tintinnid ciliates. *Journal of Plankton Research*, **40**(3): 209-221, https://doi.org/10.1093/plankt/fby011.

Shao Q W, Lin Z Z, Xu Z H et al. 2023. Integrated biogeography and assembly mechanisms of microeukaryotic communities in coastal waters near shellfish cultivation. *Microbial Ecology*, **86**(4): 2560-2573, https://doi.org/10.1007/s00248-023-02256-0.

Sloan W T, Lunn M, Woodcock S et al. 2006. Quantifying the roles of immigration and chance in shaping prokaryote community structure. *Environmental Microbiology*, **8**(4): 732-740, https://doi.org/10.1111/j.1462-2920.2005.00956.x.

Smith T W, Lundholm J T. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography*, **33**(4): 648-655, https://doi.org/10.1111/j.1600-0587.2009.06105.x.

Stegen J C, Lin X J, Fredrickson J K et al. 2013. Quantifying community assembly processes and identifying features that impose them. *The ISME Journal*, **7**(11): 2069-2079, https://doi.org/10.1038/ismej.2013.93.

Stoeck T, Hayward B, Taylor G T et al. 2006. A multiple PCR-primer approach to access the microeukaryotic diversity in environmental samples. *Protist*, **157**(1):

31-43, https://doi.org/10.1016/j.protis.2005.10.004.

Sun P, Huang L Y, Xu D P et al. 2017. Marked seasonality and high spatial variation in estuarine ciliates are driven by exchanges between the 'abundant' and 'intermediate' biospheres. *Scientific Reports*, **7**(1): 9494, https://doi.org/10.1038/s41598-017-10308-y.

Sun P, Huang L Y, Xu D P et al. 2019. Integrated space-time dataset reveals high diversity and distinct community structure of ciliates in mesopelagic waters of the Northern South China Sea. *Frontiers in Microbiology*, **10**: 2178, https://doi.org/10.3389/fmicb.2019.02178.

Sun P, Wang Y, Laws E et al. 2020. Water mass-driven spatial effects and environmental heterogeneity shape microeukaryote biogeography in a subtropical, hydrographically complex ocean system—a case study of ciliates. *Science of the Total Environment*, **706**: 135753, https://doi.org/10.1016/j.scitotenv.2019.135753.

Sun P, Yu G, Chen Z Z et al. 2015. Diagnostic model construction and example analysis of habitat degradation in enclosed bay: III. Sansha Bay habitat restoration strategy. *Chinese Journal of Oceanology and Limnology*, **33**(2): 477-489, https://doi.org/10.1007/s00343-015-4169-8.

Suzzi A L, Gaston T F, McKenzie L et al. 2022. Tracking the impacts of nutrient inputs on estuary ecosystem function. *Science of the Total Environment*, **811**: 152405, https://doi.org/10.1016/j.scitotenv.2021.152405.

Taylor W D. 1986. The effect of grazing by a ciliated protozoan on phosphorus limitation of heterotrophic bacteria in batch culture. *The Journal of Protozoology*, **33**(1): 47-52, https://doi.org/10.1111/j.1550-7408.1986.tb05554.x.

Vidussi F, Mostajir B, Fouilland E et al. 2011. Effects of experimental warming and increased ultraviolet B radiation on the Mediterranean plankton food web. *Limnology and Oceanography*, **56**(1): 206-218, https://doi.org/10.4319/lo.2011.56.1.0206.

Wan Y Y, Zhao F, Filker S et al. 2024. Parasitic taxa are key to the vertical stratification and community variation of pelagic ciliates from the surface to the abyssopelagic zone. *Environmental Microbiome*, **19**(1): 85, https://doi.org/10.1186/s40793-024-00630-0.

Wang C F, Li H B, Dong Y et al. 2021a. Planktonic ciliate trait structure variation over Yap, Mariana, and Caroline seamounts in the tropical western Pacific Ocean. *Journal of Oceanology and Limnology*, **39**(5): 1705-1717, https://doi.org/10.1007/s00343-021-0476-4.

Wang C F, Wang X Y, Wei Y Y et al. 2023a. Pelagic ciliate (Ciliophora) communities in the Southern Ocean: bioindicator to water mass, habitat suitability classification and potential response to global warming. *Progress in Oceanography*, **216**: 103081, https://doi.org/10.1016/j.pocean.2023.103081.

Wang C F, Xu M Q, Xuan J et al. 2021b. Impact of the warm eddy on planktonic ciliate, with an emphasis on tintinnids as bioindicator species. *Ecological Indicators*, **133**: 108441, https://doi.org/10.1016/j.ecolind.2021.108441.

Wang J, Zhu T Y, Pang Y et al. 2020a. Study on sources of inorganic nitrogen pollution in Minjiang estuary coastal waters. *Sichuan Environment*, **39**(6): 15-23, https://doi.org/10.14034/j.cnki.schj.2020.06.004. (in Chinese with English abstract)

Wang J J, Beusen A H W, Liu X C et al. 2020b. Aquaculture production is a Large, spatially concentrated source of nutrients in Chinese freshwater and coastal seas. *Environmental Science & Technology*, **54**(3): 1464-1474, https://doi.org/10.1021/acs.est.9b03340.

Wang W L, Huo Y L, Wang L Q et al. 2023b. Integrated assessment of trace elements contamination in sediments of a typical aquaculture bay in China: ecological toxicity, sources and spatiotemporal variation. *Journal of Cleaner Production*, **425**: 139122, https://doi.org/10.1016/j.jclepro.2023.139122.

Wang X, Liu Y F, Guo W. 2019a. Evaluation of environmental quality and change trend in Sansha Bay mariculture area in recent ten years. *Journal of Fisheries Research*, **41**(6): 519-525, https://doi.org/10.14012/j.cnki.fjsc.2019.06.009. (in Chinese with English abstract)

Wang Y B, Zhang W J, Lin Y S et al. 2014. Phosphorus, nitrogen and chlorophyll-*a* are significant factors controlling ciliate communities in summer in the northern Beibu Gulf, South China Sea. *PLoS One*, **9**(7): e101121, https://doi.org/10.1371/journal.pone.0101121.

Wang Y F, Cadotte M W, Chen Y X et al. 2019b. Global evidence of positive biodiversity effects on spatial ecosystem stability in natural grasslands. *Nature Communications*, **10**(1): 3207, https://doi.org/10.1038/s41467-019-11191-z.

Wei G S, Li M C, Li F G et al. 2016. Distinct distribution patterns of prokaryotes between sediment and water in the Yellow River estuary. *Applied Microbiology and Biotechnology*, **100**(22): 9683-9697, https://doi.org/10.1007/s00253-016-7802-3.

Welschmeyer N A. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *Limnology and Oceanography*, **39**(8): 1985-1992, https://doi.org/10.4319/lo.1994.39.8.1985.

Wen S W, Cheng Z J, Li G et al. 2025. Distribution patterns and driving mechanisms of ciliate communities from continental shelf to deep basin of the Northeastern South China Sea. *Journal of Plankton Research*, **47**(5): fbaf020, https://doi.org/10.1093/plankt/fbaf020.

Wu F X, Huang H H, Dai M et al. 2017. Spatial and temporal pattern of planktonic ciliate community and its relationship with its environment in Dapeng Cove, the South China Sea. *South China Fisheries Science*, **13**(1): 1-9, https://doi.org/10.3969/j.issn.2095-0780.2017.01.001. (in Chinese with English abstract)

Wu F X, Huang H H, Huang J R et al. 2016. Spatial pattern of the planktonic ciliate community in spring in Baisha Bay, South China Sea, and its relationship with its environment. *Journal of Tropical Oceanography*, **35**(3): 79-86, https://doi.org/10.11978/2015096. (in Chinese with English abstract)

Wu H Y, Fu S F, Wu J et al. 2021. Spatiotemporal variation of benthic biodiversity under persistent and extreme human disturbances in the Xiamen sea area, China. *Ocean & Coastal Management*, **207**: 105556, https://doi.

org/10.1016/j.ocecoaman.2021.105556.

Wu J M, Niu L H, Li Y et al. 2025. Stability characteristics of bacterial and protistan communities along an estuarine continuum: diversity, composition and co-occurrence networks. *Environmental Research*, **269**: 120920, https://doi.org/10.1016/j.envres.2025.120920.

Wu W X, Lu H P, Sastri A et al. 2018. Contrasting the relative importance of species sorting and dispersal limitation in shaping marine bacterial versus protist communities. *The ISME Journal*, **12**(2): 485-494, https://doi.org/10.1038/ismej.2017.183.

Xian W D, Ding J J, Chen J H et al. 2024. Distinct assembly processes structure planktonic bacterial communities among near- and offshore ecosystems in the Yangtze River estuary. *Microbial Ecology*, **87**(1): 42, https://doi.org/10.1007/s00248-024-02350-x.

Xiao H, Guo X G, Wu R S. 2002. Summarization of studies on hydrographic characteristics in Taiwan Strait. *Journal of Oceanography in Taiwan Strait*, **21**(1): 126-138. (in Chinese with English abstract)

Xie B, Huang J J, Huang C et al. 2020. Stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of suspended particulate organic matter as indicators for fish cage culture pollution in Sansha Bay, China. *Aquaculture*, **522**: 735081, https://doi.org/10.1016/j.aquaculture.2020.735081.

Xu H L, Jiang Y, Al-Rasheid K A S et al. 2011. Spatial variation in taxonomic distinctness of ciliated protozoan communities at genus-level resolution and relationships to marine water quality in Jiaozhou Bay, northern China. *Hydrobiologia*, **665**(1): 67-78, https://doi.org/10.1007/s10750-011-0604-9.

Xu Y, Chen X Y, Zhang J W et al. 2022. Regional and local environment drive biogeographic patterns in intertidal microorganisms. *Journal of Biogeography*, **49**(8): 1576-1585, https://doi.org/10.1111/jbi.14460.

Xu Z M, Li Y F, Lu Y H et al. 2020. Impacts of the Zhe-Min Coastal Current on the biogeographic pattern of microbial eukaryotic communities. *Progress in Oceanography*, **183**: 102309, https://doi.org/10.1016/j.pocean.2020.102309.

Yan L, Chen S Q, Wu J B et al. 2024. Characters of annual variation and seasonal variation of main chemical elements in water quality of Jiulong River estuary. *Ocean Development and Management*, **41**(3): 61-71, https://doi.org/10.20016/j.cnki.hykfygl.20240307.001. (in Chinese with English abstract)

Yan X L, Zhai W D, Hong H S et al. 2012. Distribution, fluxes and decadal changes of nutrients in the Jiulong River estuary, Southwest Taiwan Strait. *Chinese Science Bulletin*, **57**(18): 2307-2318, https://doi.org/10.1007/s11434-012-5084-4.

Yang J Y, Wu D X, Lin X P. 2008. On the dynamics of the South China Sea warm current. *Journal of Geophysical Research*: *Oceans*, **113**(C8): C08003, https://doi.org/10.1029/2007JC004427.

Yang Y B. 2020. Status quo of land-based sewage outlet and nitrogen and phosphorus discharge in the Minjiang estuary. *Ocean Development and Management*, **37**(3): 36-40, https://doi.org/10.3969/j.issn.1005-9857.2020.03.008.

Yang Y F, Li C H, Nie X P et al. 2004. Development of mariculture and its impacts in Chinese coastal waters. *Reviews in Fish Biology and Fisheries*, **14**(1): 1-10, https://doi.org/10.1007/s11160-004-3539-7.

Yi J, Lo L S H, Cheng J P. 2020. Dynamics of microbial community structure and ecological functions in estuarine intertidal sediments. *Frontiers in Marine Science*, **7**: 585970, https://doi.org/10.3389/fmars.2020.585970.

Yu X W, Gao X Y, Shang L et al. 2023. Spatial and temporal change determined co-occurrence networks stability and community assembly processes of epipelagic seawater microbial community in the Nordic Sea. *Science of the Total Environment*, **859**: 160321, https://doi.org/10.1016/j.scitotenv.2022.160321.

Yu X W, Li X R, Liu Q et al. 2022. Community assembly and co-occurrence network complexity of pelagic ciliates in response to environmental heterogeneity affected by sea ice melting in the Ross Sea, Antarctica. *Science of the Total Environment*, **836**: 155695, https://doi.org/10.1016/j.scitotenv.2022.155695.

Yu Y, Zhang W C, Wang S W et al. 2013. Abundance and biomass of planktonic ciliates in the sea area around Zhangzi Island, Northern Yellow Sea. *Acta Ecologica Sinica*, **33**(1): 45-51, https://doi.org/10.1016/j.chnaes.2012.12.007.

Yuan M M, Guo X, Wu L W et al. 2021. Climate warming enhances microbial network complexity and stability. *Nature Climate Change*, **11**(4): 343-348, https://doi.org/10.1038/s41558-021-00989-9.

Yvon-Durocher G, Allen A P. 2012. Linking community size structure and ecosystem functioning using metabolic theory. *Philosophical Transactions of the Royal Society B*: *Biological Sciences*, **367**(1605): 2998-3007, https://doi.org/10.1098/rstb.2012.0246.

Zander A, Bersier L F, Gray S M. 2017. Effects of temperature variability on community structure in a natural microbial food web. *Global Change Biology*, **23**(1): 56-67, https://doi.org/10.1111/gcb.13374.

Zhang C R, Liu Q, Li X R et al. 2021. Spatial patterns and co-occurrence networks of microbial communities related to environmental heterogeneity in deep-sea surface sediments around Yap Trench, Western Pacific Ocean. *Science of the Total Environment*, **759**: 143799, https://doi.org/10.1016/j.scitotenv.2020.143799.

Zhang C X, Zhang W C, Ni X B et al. 2015. Influence of different water masses on planktonic ciliate distribution on the East China Sea shelf. *Journal of Marine Systems*, **141**: 98-111, https://doi.org/10.1016/j.jmarsys.2014.09.003.

Zhao F, Filker S, Xu K D et al. 2017. Patterns and drivers of vertical distribution of the ciliate community from the surface to the abyssopelagic zone in the western Pacific Ocean. *Frontiers in Microbiology*, **8**: 2559, https://doi.org/10.3389/fmicb.2017.02559.

Zhao F, Xu K D. 2016. Molecular diversity and distribution pattern of ciliates in sediments from deep-sea hydrothermal vents in the Okinawa Trough and adjacent sea areas. *Deep Sea Research Part I*: *Oceanographic Research Papers*, **116**: 22-32, https://doi.org/10.1016/j.

dsr.2016.07.007.

Zheng H D. 2019. Constructing and evaluating an index system for aquaculture carrying capacity in Dongshan Bay. *Journal of Fisheries Research*, **41**(5): 393-398, https://doi.org/10.14012/j.cnki.fjsc.2019.05.005. (in Chinese with English abstract)

Zheng X H. 2010. Changes in nitrogen, phosphate, and eutrophication characteristics in the Minjiang estuary. *Journal of Oceanography in Taiwan Strait*, **29**(1): 42-46, https://doi.org/10.3969/J.ISSN.1000-8160.2010.01.007. (in Chinese with English abstract)

Zhou J Z, Ning D L. 2017. Stochastic community assembly: does it matter in microbial ecology? *Microbiology and Molecular Biology Reviews*, **81**(4): e00002-17, https://doi.org/10.1128/MMBR.00002-17.

Zhou X T, Lennon J T, Lu X et al. 2023. Anthropogenic activities mediate stratification and stability of microbial communities in freshwater sediments. *Microbiome*, **11**(1): 191, https://doi.org/10.1186/s40168-023-01612-z.

Zhu D Y. 2013. A study on the origin and oscillation of near-bottom warm water near Pingtan Island in winter 2007. *Journal of Applied Oceanography*, **32**(4): 480-487, https://doi.org/10.3969/J.ISSN.2095-4972.2013.04.005. (in Chinese with English abstract)

Zhu J W, Ma Y F, Huang L F et al. 2022. Homogeneous selection is not always important in bacterial community in the eutrophic enclosed bay. *Ecological Processes*, **11**(1): 27, https://doi.org/10.1186/s13717-022-00373-1.

Zou S Y. 2022. Characteristics of phytoplankton and its Pearson correlation with environmental factors in Pingtan inshore sea area, Fujian Province from spring to summer. *Journal of Fisheries Research*, **44**(3): 266-274, https://doi.org/10.14012/j.cnki.fjsc.2022.03.009. (in Chinese with English abstract)

Electronic supplementary material

Supplementary material (Supplementary Tables S1–S5 and Fig.S1) is available in the online version of this article at https://doi.org/10.1007/s00343-026-5387-y.