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Niche features and assembly mechanisms of microeukaryotic generalists and specialists along a north—south gradient of a subtropical coastal sea

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ABSTRACT: The assembly mechanisms of generalists and specialists have been extensively studied for prokaryotes but underexplored for microeukaryotes, the crucial players in marine ecosystems. In addition, the latitudinal gradient of biodiversity on the scale of the global ocean has been well documented, but is less studied at a regional scale. Here, we investigated plankton assemblages along a latitudinal gradient of a subtropical regional coastline using high-throughput sequencing of the 18S rRNA gene (rDNA) V4 region. We observed a trend of increasing diversity with decreasing latitudes in this provincial spatial scale, resembling the previously reported globalscale trend. Based on niche breadth, microeukaryotes in our samples were grouped into generalists, opportunists and specialists. Generalists were more influenced by selection than specialists, with temperature being an important factor. In addition, we found that dispersal limitation had a greater influence on the generalists than on the specialists. Interestingly, dinoflagellates, a major component in both generalist and specialist subcommunities, were important to stabilization in the generalist subcommunity. Chlorophyta, in contrast, had a crucial effect on network stability for specialists. Overall, this study verifies the latitudinal gradient of biodiversity at a mesoscale, and provides new insights into the ecotypic grouping and assembly mechanism of microeukaryotes. It also sheds light on the potential differential importance of Dinoflagellata and Chlorophyta.

KEY WORDS: Microeukaryotic community \cdot Subtropical sea region \cdot Diversity \cdot Assembly mechanisms \cdot Generalists and specialists \cdot Co-occurrence patterns

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1. INTRODUCTION

Microbial communities are assembled by deterministic and stochastic processes (Logares et al. 2013, Liu et al. 2015, K. Wang et al. 2015, Yang et al. 2016, Liao et al. 2017, Mo et al. 2018, 2021). Deterministic processes include environmental filtering (temperature, salinity, nutrients) and species interactions (predation, parasitism, mutualism and competition) (Chesson 2000, Fargione et al. 2003). By contrast, stochastic 36

processes include dispersal limitation, mass effects, speciation and random birth and death rates that shape community composition, and in these processes, all species are equal (Chave 2004, Hubbell 2005). Notably, species interactions are not included in stochastic processes.

Based on their ecological niche breadths, i.e. how plastic or adaptive they are to environmental disturbances, microbes may behave as generalists or specialists (Pandit et al. 2009). Generalists have broader niche breadths and can tolerate varying environments, while specialists have narrower niche breadths and are stronger competitors (Levins 1968, Pandit et al. 2009). Many studies have examined the importance of prokaryotic microbial generalists and specialists in different ecosystems (Sriswasdi et al. 2017, Mo et al. 2021, Xu et al. 2022a). It has been found that microbial generalists and specialists are primarily shaped by deterministic processes, and selection has stronger effects on specialists than on generalists (Mo et al. 2021, Xu et al. 2022a). Specialists are important to ecosystems because their decline can result in community homogenization and diversity decreases, endangering ecosystem services (Clavel et al. 2011). It has been postulated that specialists may decline faster than generalists in response to climate and environmental changes due to their higher extinction risks (Thuiller et al. 2005).

The community structure of microeukaryotes influences nutrient interactions, food web structure and the potential of carbon fixation (Dossena et al. 2012, Mouw et al. 2016, Brander & Kiørboe 2020) and may be shaped by different ecological processes from that of prokaryotes (Gad et al. 2020, Liu et al. 2020). Hence, unraveling the differences in the mechanisms that shape the community assembly of microeukaryotic generalists and specialists is important both for understanding how the plankton community responds to environmental changes and for informing biodiversity conservation. However, although some studies have investigated processes that shape the assemblies of freshwater microeukaryotic communities (Abdullah Al et al. 2022) or marine picoeukaryotic communities (Logares et al. 2020), the findings are not consistent as to the relative importance of stochastic and deterministic processes. Therefore, the ecological differentiation of microeukaryotic generalists and specialists in marine environments remains to be elucidated.

Interactions between organisms are vital to the function of the community and are typically inferred from co-occurrence patterns (Faust & Raes 2012) revealed by network analysis (Gilbert et al. 2012).

Mo et al. (2021) reported that the co-occurrence patterns in bacterial generalists and specialists were non-random and that the specialists showed a more robust network structure than the generalists. Network characteristics can also influence how the community responds to environmental changes, and weak associations may result in unstable networks (Coyte et al. 2015, Kuiper et al. 2015). Previous research has found that archaea play a key role in the construction of microbial interactive networks in soil (Shi et al. 2019), and fungi were found to stabilize multi-kingdom networks in a high-elevation ecosystem (Yang et al. 2022). Such inquiries are limited for marine microeukaryotes, where major phyla such as dinoflagellates and diatoms play pivotal roles in community structure and function. Dinoflagellates are one of the most important primary producers in the ocean and the greatest contributors of harmful algae blooms (Jeong et al. 1999). Their ecological success is in part attributable to their diversified trophic modes, ranging from autotrophy to mixotrophy to heterotrophy (Jeong et al. 2010). Diatoms (Bacillariophyta) are another dominant group of primary producers (Yool & Tyrrell 2003) that play an important role in the food web and silicon cycle (Ragueneau et al. 2006). Comparatively, green algae (Chlorophyta) are less studied in the ocean (Tragin et al. 2016) but are prevalent in coastal waters (Tragin et al. 2018). Considering their ecological importance, whether dinoflagellates, diatoms and green algae will influence network stability in the marine microeukaryotic community needs to be determined. Therefore, a significant knowledge gap exists in understanding the interactive networks of microeukaryotic generalists and specialists and the roles of dominant lineages.

Here, to address the knowledge gap presented above, a study was conducted at a mesoscale in a subtropical coastal sea covering 3752 km of coastline and crossing 3° in latitude. The main objectives were to profile the microeukaryotic community in terms of latitudinal patterns of diversity, composition of generalists and specialists and their respective community assembly mechanisms and to identify major lineages that are critical to the stability of their associated interactive networks. We aimed to use the results to examine 3 hypotheses: (1) the regional north-south gradient of coastal microeukaryotic biodiversity is mainly driven by the direct effect of temperature; (2) both generalists and specialists are assembled by stochastic processes; and (3) the co-occurrence networks of generalists and specialists can be stabilized by different lineages.

2. MATERIALS AND METHODS

2.1. Study area, sampling and physico-chemical analysis

This study investigated 5 coastal bays in the East China Sea system, which are located from the north (26.7262° N, 119.7427° E) to the south (23.6149° N, 117.5383° E) of Fujian province, covering 3752 km. These included, from south to north, Dongshan Bay Area (DS), Xiamen Sea Area (XM), Pingtan Bay Area (PT), Minjiang Estuary (MJ) and Sansha Bay Area (SS) (see Fig. 1). A synchronized field campaign was launched in May 2020 using 5 research vessels, each cruising in one of the 5 ecosystems. A range of 14-28 stations were sampled in each area. Both surface (0.5-2 m) and bottom (5-72 m) water samples were collected. Seawater was first pre-filtered through a sieve (200 µm pore) to remove meso- and macrozooplankton as well as debris and sediment, then about 300–1000 ml of seawater was filtered through polycarbonate membranes (3 µm pore, 47 mm diameter; Millipore). The membranes retaining the plankton cells were placed in sterile 2 ml centrifuge tubes. Samples were immediately stored at -80°C until DNA extraction.

Eight environmental parameters were measured. Water temperature, depth and salinity were measured through a conductivity-temperature-depth (CTD) oceanic profiler. To measure the nutrients, water samples were filtered through 0.45 µm poresize cellulose acetate filters. An AA3 AutoAnalyzer (Bran-Luebbe) was used to measure nitrate (NO_3^-) , nitrite (NO_2^{-}) , ammonium (NH_4^{+}) , silicate (SiO_4^{4-}) and phosphate (PO_4^{3-}) based on the pink azo dye spectrophotometric method, the indophenol blue method and the molybdenum blue method, respectively (Dick & Tabatabai 1977, Pai et al. 2001, Dai et al. 2008, Yan et al. 2012). About 200-400 ml of seawater was filtered through GF/F membranes (25 mm diameter) and acetone was added to extract the chlorophyll *a*, which was determined with a Turner Trilogy fluorometer (Welschmeyer 1994). Detailed sample information and environmental factors determined are shown in Table S1 in the Supplement at www.intres.com/articles/suppl/m742p035 supp.pdf.

2.2. DNA extraction, PCR and sequencing

DNA extraction was conducted as described in a previous study (Yuan et al. 2015). Briefly, membranes with plankton cells were cut into small pieces and

soaked in 1 ml lysis buffer (10 mM Tris, 100 mM EDTA, 0.5% SDS). The samples were incubated at 56°C for about 2 d. Next, bead-beating was performed on a FastPrep-24 bead mill (MP Biomedicals) at 6 m s^{-1} for 1 min. This step was repeated 3 times, and during the 5 min intervals between the cycles, the samples were placed on ice to eliminate the foam. To each sample, 165 μ l of 5 M NaCl and 165 μ l of 10% CTAB (cetyl/ hexadecyl trimethyl ammonium bromide, in 0.7 M NaCl solution) was added. The samples were then incubated at 56°C for 10 min. Each sample was equally split in two, and to each half, 665 µl chloroform was added. The tubes were vortexed and centrifuged at ca. $13523 \times g$ for 10 min. Only the upper layer was transferred to a new tube. Total genomic DNA was extracted and purified using the DNA Clean & ConcentratorTM-25 kit (Zymo Research). Binding buffer (2× volume of the upper layer) was added to each tube and loaded into the columns. The columns were centrifuged at ca. $13523 \times g$ for 30 s. Then, 200 µl wash buffer was added to each column, and they were centrifuged at ca. 13 523 × *g* for 30 s. Finally, 30 μl of 10 mM Tris-HCl was added to the columns to elute the DNA. DNA concentration and purity were assessed using a Nanodrop 2000 Spectrophotometer (Thermo Scientific). 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)GCG GTA ATT CC-3') and TAReukREV3 (5'-ACT TTC GTT CTT GAT(C/T)(A/G)A-3') (Stoeck et al. 2006). The polymerase chain reaction (PCR) protocol consisted of an initial denaturation at 94°C for 30 s; followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s and elongation at 72°C for 30 s; and a final elongation step at 72°C for 5 min. The PCR products were purified using Cycle Pure Kit (100) OMEGA (New England Biolabs). The amplicons were used for the construction of libraries, which were qualitychecked and sequenced (PE250) on an Illumina Novaseq 6000 platform (Illumina).

2.3. Amplicon sequence variant classification

Raw reads with low-quality bases were removed using Trimmomatic v.3.3 (Bolger et al. 2014). Adaptors and primer sequences were trimmed using Cutadapt (Martin 2011) (v.1.9.1). The resulting good-quality sequences were assembled using USEARCH (Edgar 2013) (v.10). Identification and removal of chimeras was also conducted using UCHIME (Edgar et al. 2011) (v.8.1). The DADA2 (Callahan et al. 2016) method in QIIME2 (Crépineau et al. 2000) (v.2020.06) Author copy

was applied to de-noise sequences to generate amplicon sequence variants (ASVs). Species annotation was carried out based on the Protist Ribosomal Reference Sequence Database (v.4.14.1) (Guillou et al. 2012) using an 80% confidence threshold.

2.4. Identification of generalists and specialists

Generalists and specialists were identified following a previous study (Sriswasdi et al. 2017). The ASV table was randomly shuffled 10 000 times while the observed ASV richness was maintained in each sample. The random distribution of the ASVs was then compared with the observed distribution. Two thresholds were obtained from the comparisons. Based on the comparisons, the ASVs enriched in wide environments were defined as generalists, and those enriched in narrow environments were defined as specialists. The ASVs that occurred between the 2 thresholds were identified as opportunists. The detailed classification of generalists and specialists as well as the confidence of ASVs assigned to the species level are shown in Table S2.

2.5. Community diversity analysis

Alpha diversity indices, including Chao 1 (representing richness) and the Shannon-Wiener diversity index (representing richness and evenness), were calculated in QIIME2 (Bolyen et al. 2019). The Chao 1 index was based on the equation:

Chao 1 = S +
$$\frac{n_1(n_1 - 1)}{2(n_2 + 1)}$$
 (1)

(Chao 1984), where *S* is the number of ASVs, n_1 is the number of ASVs with one sequence and n_2 is the number of ASVs with 2 sequences. The Shannon-Wiener index was based on ASV abundance and the Chao 1 index. To uncover the microeukaryotic community differences, non-metric multidimensional scaling (NMDS) ordination was constructed for generalists and specialists (Clarke & Gorley 2006). An analysis of similarity (ANOSIM) was used to test significant differences in communities, using the 'vegan' package in R (v.4.2.1) (Clarke & Gorley 2006, R Core Team 2018). The global R value in ANOSIM ranges from 0 to 1 and represents the degree of separation between groups; R = 0 indicates no separation, whereas R = 1 suggests complete separation (Clarke & Gorley 2006).

The traditional community similarity indices Bray-Curtis distance and Unifrac distance were calculated in R with the 'vegan' package (Oksanen et al. 2015). The Bray-Curtis distance is 1 minus the fraction of minimum per-sample abundance of shared taxa (Bray & Curtis 1957). The Unifrac distance (weighted) is the fraction of unshared branch length on a phylogenetic tree, weighted by taxa abundances (Lozupone & Knight 2005). Taxa interaction-adjusted (TINA) and phylogenetic interaction-adjusted (PINA) indices were estimated according to Schmidt et al. (2017). The TINA index is based on a species co-occurrence network or species interaction; the PINA index is based on phylogenetic similarities (Schmidt et al. 2017). PERMANOVA analyses were performed using the ADONIS function in R with the 'vegan' package in order to calculate the amount of variance in community composition explained by environmental factors or geographic variables (province, temperature, salinity, NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-} and SiO_4^{4-}). We ran 999 permutations; only results with p < 0.05 were accepted as significant variations. Here, the 5 coastal areas were used as geographic variable factors and were then determined as the biogeographic provinces. The 5 coastal areas represent 5 different provinces, respectively.

A total of 135 dinoflagellate sequences were selected for phylogenetic analysis. We retrieved 34 reference sequences of common dinoflagellate species from NCBI. The phylogenies were used to investigate the dinoflagellate diversity and their phylogenetic positions. Alignment of multiple sequences was performed using MUSCLE. MEGA-X was used to construct the tree. A maximum likelihood (ML) tree was obtained through the GTR+G model. An *Amoebophrya* species was used as an outgroup to root the tree. A bootstrap approach was carried out with 1000 resamplings for the ML tree in order to assess the species grouping robustness.

2.6. Network construction and C-score estimation

Network analysis was carried out with the iNAP platform (Feng et al. 2022) to examine the co-occurrence patterns of taxa in generalist and specialist networks as well as the stability of multi-phylum networks of Dinoflagellata, Bacillariophyta, Arthropoda, Chlorophyta and Ciliophora. FastSpar (Friedman & Alm 2012, Watts et al. 2019) was used to calculate the pairwise correlations between plankton ASVs, and only correlations with $|\mathbf{r}| > 0.6$ and a statistical significance of p < 0.01 were retained for the network. Among all nodes, the network hubs (*z*-score > 2.5; p-score [participation coefficient] > 0.62), module hubs (z-score > 2.5; p-score < 0.62), connectors (zscore < 2.5; p-score > 0.62) and peripherals (z-score < 2.5; p-score < 0.62) were identified (Strogatz 2001, Guimera 2005). All nodes defined as hubs and connector nodes could be recognized as potential keystone species in co-occurrence networks (Shi et al. 2016). Network visualization was conducted using Gephi (v.0.9.7). The topological characteristics of the networks, including average degree, average path length, graph diameter, graph density, clustering coefficient and modularity, were calculated in R using the 'igraph' package (Csardi 2013). Network stability was assessed by natural connectivity, and the nodes were gradually removed to evaluate how quickly robustness would be degraded (Peng & Wu 2016). The lower the absolute value of the slope of the natural connectivity versus the number of node plots, the more stable the network (Wu et al. 2021).

The checkerboard score (C-score) was calculated in R (v.4.2.1) (R Core Team 2018) with the 'EcoSimR' package (Ellison 2013). This variable was used to evaluate whether the real distributions of ASVs are random or not. The ASV table was modified to a binary matrix of presence (1) and absence (0), and then the C-score was calculated under the null model (Gotelli & McCabe 2002). If the C-score is larger than the one expected by chance, the species distributions are considered non-random (Sanders et al. 2007). The standardized effect sizes (SES) for C-score were calculated through the formula:

$$SES = \frac{observed C-score - mean simulated C-score}{standard deviation of simulated C-scores}$$
(2)

(Gotelli & McCabe 2002). Positive SES values mean that it is less likely to be a random pattern, which indicates the predominance of segregation within communities. Contrarily, if SES values are negative, this implies the predominance of facilitation. If co-occurrence patterns are the same as what random patterns expect, values of SES should be between -2 and +2 (Mo et al. 2021).

2.7. Quantification of ecological assembly processes based on null model and dispersal–niche continuum index

To quantify and compare the community assembly of generalists and specialists, a null model was built based on Stegen et al. (2013). The deterministic and stochastic processes are classified according to the beta nearest taxon index (β NTI), which is the difference between the observed mean nearest taxon distance (β MNTD) and the mean of the null distribution of β MNTD normalized using its standard deviation (Mo et al. 2021). The β MNTD was calculated to evaluate pairwise phylogenetic turnover between communities using the 'picante' package in R (Webb et al. 2002, Stegen et al. 2013). If the absolute value of β NTI $(|\beta NTI|)$ is ≥ 2 , which indicates a significant deviation, the process is considered a deterministic process; contrarily, $|\beta NTI| < 2$ suggests stochastic processes (Dini-Andreote et al. 2015). When $\beta NTI \ge 2$, heterogeneous selection is dominant in community turnover; when $\beta NTI < -2$, homogeneous selection dominates the community turnover. The Bray-Curtis-based Raup-Crick metric (RCbray) index was further calculated for pairwise comparisons with $|\beta NTI| < 2$ (Stegen et al. 2013). $|\beta NTI| < 2$ and RCbray < -0.95 or $|\beta NTI| < 2$ and RCbray > 0.95 indicates homogenizing dispersal and dispersal limitation, respectively. $|\beta NTI| < 2$ and [RCbray] < 0.95 indicated undominated community turnover, which means that the community is dominated neither by dispersal nor selection.

The dispersal—niche continuum indices (DNCI) were calculated to determine the level of the assembly process. Positive DNCI values suggest a dominance of niche processes and negative DNCI values imply the role of dispersal (Wen et al. 2022). The absolute value of DNCI represents the level of the 2 processes. The analysis was performed in R using the 'DNCImper' package (v.0.0.1.0000) (Gibert et al. 2020). The pairwise DNCI values among the 5 different bays were compared using the function 'DNCI_multigroup'.

3. RESULTS

3.1. Spatial dynamics of environmental variables and forcing factors

The sampling sites were located along the coastlines of Fujian province. The climate of Fujian province is subtropical maritime monsoon, with an average temperature range from $17^{\circ} - 22^{\circ}$ C. The average precipitation ranges from 1200-1700 mm. Regarding the 5 areas, DS is an important mariculture harbor; XM is an island city surrounded by coastal water, harboring a variety of marine species; MJ has a special ecological environment, as it is abundant in organic matter and nutrients; and SS is a typical aquaculture harbor, which has created eutrophic conditions (Han et al. 2021).

A series of environmental factors characterizing the 5 coastal areas (from south to north: DS, XM, PT, MJ and SS) is visualized in Fig. S1. The 5 areas differed in temperature, which was much higher in the south than

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Situated along the Taiwan Strait, our sampling area is influenced by several environmental forcing factors (Fig. 1), including the high northward flow of the South China Sea Warm Current in summer (Yang et al. 2008). The influence of the Zhe-Min Coastal Current (ZMCC) is generally stronger in winter than in summer (Xu et al. 2020). The South China Sea is also intruded by the Kuroshio Current in both summer and winter (Guo et al. 2019).

3.2. Composition and classification of the microeukaryotic communities

A total of 46234085 raw rRNA gene reads were obtained from all 578 samples in the 5 coastal areas of southeast China that we surveyed in May of 2020 (Fig. 1). After de-noising through the DADA2 pipeline, 1295 ASVs were obtained from all the samples. Following elimination of those ASVs annotated as unassigned species, 1241 ASVs were kept for further analysis. Based on the criteria described in Section 2.4, species occurring in fewer than 93 environments were identified as specialists and those occurring in more than 136 environments were identified as generalists (Fig. 2a). Of the 1241 ASVs retrieved from the 5 bays, 423 ASVs were identified as generalists and 603 ASVs as specialists, representing 85.5 and 8.91% of the total sequences, respectively. The richness of specialists was higher than that of generalists, while the relative abundance of specialists was only approximately one-tenth that of the generalists. Although 419 generalist ASVs (99%) were shared in all 5 coastal areas, only 318 specialist ASVs (52.7%) occurred in all 5 coastal areas (Fig. 2b). No ASV was simultaneously classified as a generalist and a specialist, indicating that the defining criteria used were appropriate.

The most abundant groups in the generalist community (GRL) were Dinoflagellata (23.25–30.07%) and Arthropoda (14.20–34.87%), followed by Bacillariophyta (7.33–22.42%), Chlorophyta (1.08– 11.53%) and Ciliophora (2.96–5.89%) (Fig. S2b). For the specialist community (SPL), Dinoflagellata was most abundant (17.02–25.82%), followed by Ciliophora (4.86–23.71%), Bacillariophyta (4.94–13.69%), Arthropoda (5.50–16.49%) and Chlorophyta (0.75– 4.87%) (Fig. S2c). The relative abundance of Arthropoda was much higher in GRL than in SPL, while that of Ciliophora was higher in SPL. Generally, the relative abundance of these main taxa was lower in the northern bays (PT and SS) and higher in the southern bays (DS and XM) except that they were also abundant in MJ, which is situated in the north.

Generalist dinoflagellates mostly comprised species from the Gymnodiniaceae and Kareniaceae families in the Gymnodiniales and the Syndiniales orders. The specialist dinoflagellates were mostly from the Gymnodiniaceae family in the Gymnodiniales order, the Syndiniales order and the Thoracosphaeraceae family in the Peridiniales order. The phylogenetic tree with these sequences and reference sequences indicated that the majority of these sequences belonged to diverse unclassified species in the Syndiniales order but the rest belonged to diverse unclassified species in other dinoflagellate orders (Fig. S3).

3.3. The north-south pattern of microeukaryotic diversity

Diversity indices (both Shannon-Wiener and Chao 1) calculated based on the ASVs showed a pattern of being high in the southmost area (DS) and decreasing going north to MJ (Fig. S4). An exception occurred in SS, where the diversity indices were higher than in other northern areas (PT and MJ) (Fig. S4). In geographic distribution, generalists were more abundant in SS, DS and XM than in the other study areas, while more specialists were present in SS, PT and DS than in the other areas (Fig. S4b,c,e,f). We found no significant difference between generalists and specialists with the Shannon-Wiener index, but the Chao 1 index was much higher for generalists than specialists (Fig. S5a,b). This indicated that generalists had higher species numbers than specialists but that they were similar in evenness.

Overall, the diversity indices were positively correlated with salinity and PO_4^{3-} (Fig. S6a). The high diversity in SS appeared to be a result of high PO_4^{3-} , given that the salinity in SS was not higher than the other areas and that the community composition exhibited no great difference from the other areas. The Chao 1 index of generalists was positively correlated with the abundances of PO_4^{3-} , NH_4^+ and NO_2^- (Fig. S6b). By contrast, the Chao 1 index of the specialists was more strongly correlated with temperature and salinity (Fig. S6c). The correlation between the Chao 1 index and environmental factors was stronger than that between the Shannon-Weiner index and environmental factors. To further explore the effect of high diversity in SS on the general correlations, sam-







Fig. 2. Identification of microeukaryotic generalists and specialists and comparison of microeukaryotic plankton communities among the 5 coastal areas. (a) Random/observed distribution of the amplicon sequence variant (ASV) environment. (b) Venn diagrams of the number of generalist, specialist and all ASVs in the 5 coastal areas. (c) Non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis community similarity. DS: Dongshan Area; MJ: Minjiang estuary; XM: Xiamen Area; PT: Pingtan Area; SS: Sansha Area

ples from SS were removed and correlations were analyzed again (Fig. S6d-f). After the exclusion of SS, the correlation between diversity and PO_4^{3-} became non-significant, but correlations between diversity and other nutrient factors became more significant, indi-

cating the high diversity in SS was strongly influenced by PO_4^{3-} nutrient availability. This has a strong impact on the general south—north trend of diversity. Scatter plots showing Spearman's rank correlations between alpha diversity indices and en-

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vironmental factors for all sampling sites with SS included or excluded are shown in Fig. S7.

3.4. Spatial variations and influencing environmental factors of the microeukaryotic community

According to the NMDS analysis based on Bray-Curtis community similarity (Fig. 2c), the 5 communities were distributed in a clear trend from south to north. The communities in DS and XM were separated from communities in the other 3 areas in the north. Our results also showed that the microeukaryotic communities were generally uniform between surface and bottom layers (Fig. S8a) (ANOSIM, R = 0.000168, p = 0.4438). Similar results were obtained for the generalists (ANOSIM, R = -0.002268, p = 0.5418) and specialists (ANOSIM, R = 0.01829, p = 0.0368) (Fig. S8b,c).

Both generalists and specialists were found to be correlated with environmental factors (Fig. S9) (Mantel test, p < 0.01). β -diversity was estimated based on community dissimilarity. We calculated the percentage of variance explained by 8 different environmental factors, as captured by the β -diversity indices TINA (based on species co-occurrence network or species interaction), PINA (based on phylogenetic similarities), Bray-Curtis dissimilarity and Unifrac (Fig. 3). The TINA index explained the highest percentage of community variance for province, temperature, NH_4^+ and PO_4^{3-} . Compared to specialists, the community variance captured by TINA was higher for generalists. Among all these factors, province and temperature were the 2 main factors that influenced the community most. For generalists, temperature explained up to 45.6% and province explained up to 38.0% of the TINA index (ADONIS R²). For specialists, temperature explained up to 27.9% and province explained up to 27.2% of the TINA index (ADONIS R²). PINA explained the highest community variance for NO3- and SiO_4^{4-} . Similarly, generalists also exhibited higher community variance than specialists as explained by NO_3^- and SiO_4^{4-} captured by PINA. Meanwhile, the influences of parameters on the other 2 indices were relatively moderate. Based on the definition of the 4β -diversity indices, this result showed that temperature and province had great effects on species cooccurrence network, especially on generalists. As demonstrated by TINA analysis, temperature and province had significant impacts on species interaction. Accordingly, as indicated by PINA analysis, NO₃⁻ and SiO₄⁴⁻ were significant in the phylogenetic tree for generalists.

3.5. Ecological processes shaping the microeukaryotic plankton communities

Our analysis showed that the communities were mainly shaped by stochastic processes, and dispersal limitation contributed the highest percentage (74.7% for generalists, 62.3% for specialists). The influence of dispersal limitation was confirmed in the results of the DNCI between the 5 coastal areas: dispersal between PT and SS, DS and XM was high, indicating that it belonged to different water masses than the latter 3 communities (Fig. S10). Deterministic processes contributed more to the assembly of the generalists (21.34%) than to that of the specialists (11.98%) (Fig. 4a,b). The deterministic processes that influenced the assembly of generalists were mainly homogeneous selection, while those that influenced the assembly of specialists were mainly variable selection. The β NTI of generalists and specialists mostly varied between -2 and 2, and the indices of generalists were generally lower than those of specialists (Fig. 4c).

The β NTI indices did not differ among the 5 areas, and this result was true for both generalists and specialists (Fig. S11). Despite the dominance of stochastic processes for the microeukaryotic community, the influence of temperature on the community was not negligible. We binned the 5 areas into 2 groups: a high-temperature group (DS and XM; range: 24.79° -33.55°C) and a low-temperature group (MJ, PT and SS; range: $20.93^{\circ} - 25.14^{\circ}$ C) (Kruskal-Wallis test, p < 0.001). Nutrient conditions were not as different as temperature between the 2 groups (Fig. 5a), indicating that temperature was the major factor separating the 2 groups. Finally, the results showed that network robustness was higher in the southern group (DS + XM), where the temperature was higher (Fig. 5b). The GRL network in the northern group (PT + MJ + SS)was less stable compared to the specialists.

3.6. Co-occurrence patterns of generalists and specialists

Network analysis was conducted to study the cooccurrence patterns of both generalists and specialists. Based on the FastSpar results, the network consisted of 294 nodes (180 generalists and 114 specialists) and 3198 edges (543 among generalists, 1520 among specialists and 1135 between the 2 groups) (Fig. 6a).

The generalists formed a network made up of 153 nodes and 534 edges, while the specialist network consisted of 91 nodes and 1105 edges (Table S3). The GRL network harbored more nodes and fewer edges



Fig. 3. Main environmental factors affecting the microeukaryotic plankton community structure as captured by different β -diversity metrics between generalists and specialists (TINA and PINA: Taxa- and Phylogenetic interaction-adjusted, respectively). The x-axis shows the percentage of variance (ADONIS R²) in communities explained by different environmental factors. NO₃⁻: nitrate; NO₂⁻: nitrite; NH₄⁺: ammonium; PO₄³⁻: phosphate; SiO₄⁴⁻: silicate. Only significant results (p < 0.05) are displayed

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Fig. 4. Ecological processes of (a) generalists and (b) specialists based on the null model and (c) the beta nearest taxon index (βNTI) of generalists and specialists. In (a) and (b), inner circle: contribution of deterministic and stochastic processes; outer circle: percentage of the detailed processes. Boxplot horizontal line: median; box: interquartile range from 25th–75th percentile; whiskers: minimum and maximum values; dots: outliers

than the SPL network. The topological features of the generalist co-occurrence network differed from that of the specialist co-occurrence network. Compared to specialists, the GRL network had higher average path length, graph diameter and modularity but a lower average degree, graph density and clustering coefficient (Table S3). The results of the C-score analysis showed that the co-occurrence patterns of the networks were non-random, as the observed C-scores were higher than the C-scores expected by the null model (Table S3). In addition, the SES values were larger than 2, indicating that the patterns were nonrandom and segregation was a predominant factor.

Five major modules accounted for 79.75% and other modules accounted for 20.25% of the generalist co-occurrence network. The SPL network was slightly different, as it consisted of 6 major groups that accounted for 84.62% of the whole network with other modules making up the remaining 15.38% (Fig. 6b,c). Arthropoda, Bacillariophyta, Chlorophyta, Ciliophora and Dinoflagellata occupied most nodes in the major modules of the generalist co-occurrence network, while in SPL network, more nodes were occupied by Arthropoda, Ciliophora, Dinoflagellata and Polycystinea (Fig. S12a,b).

Four ASVs were identified as keystone species (module hubs) as defined by Strogatz (2001) in the

GRL network, including 2 from Dinoflagellata, 1 from Chlorophyta and 1 from Ochrophyta. Markedly more keystone species (connector) were found from the SPL network; in total, 39 ASVs that belonged to Polycystinea (6 ASVs), Dinoflagellata (5 ASVs), Chlorophyta (5 ASVs), Streptophyta (5 ASVs), Arthropoda (5 ASVs), Tubulinea (3 ASVs), Ochrophyta (2 ASVs), Ciliophora (2 ASVs), Annelida (1 ASV), Cercozoa (1 ASV), Cnidaria (1 ASV), Myzozoa (1 ASV), Rotifera (1 ASV) and unclassified Eukaryota (1 ASV) (Table S4). Given that both Chlorophyta (a total of 6 ASVs) and Dinoflagellata (a total of 7 ASVs) were found as keystone species, they were important sources of keystone lineages in both the generalist and specialist groups.

3.7. Role of specific taxa in network stability

Considering the dominance of dinoflagellates (Dinoflagellata), diatoms (Bacillariophyta) and green algae (Chlorophyta) in plankton as well as their crucial ecological roles in marine ecosystems, their impacts on the stability of networks were investigated. The natural connectivity versus removed nodes (%) plot describes how the absence of lineages changes connectivity (Fig. 6d,e). For generalists, connectivity



Fig. 5. Profiles of environmental factors and effects on network stability. (a) Temperature, nitrate, nitrite, ammonium, phosphate and silicate in the southern group (DS: Dongshan; XM: Xiamen) and the northern group (PT: Pingtan; MJ: Minjiang; SS: Sansha). The variables were compared through Kruskal-Wallis test; ns: p > 0.05; *p < 0.05, *p < 0.01, **p < 0.001. (b) Changes in network stability at high or low temperature for all species, generalists and specialists. The decreasing trend of natural connectivity is fitted with 80% nodes lost, and the R² and slope are shown in diagrams. The lower the absolute value of the slope, the more stable the network. Boxplot parameters as in Fig. 4

declined at the highest rate when dinoflagellates were removed (i.e. the slope decline was greatest in Fig. 6d). Comparatively, the removal of Bacillariophyta and Chlorophyta did not have much influence on the slope. Therefore, the removal of the Dinoflagellata resulted in the least stable network of generalists compared to the removal of Bacillariophyta and Chlorophyta, indicating that dinoflagellates were crucial to the network stability of generalists. For specialists, the connectivity decline slope was the highest with

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Fig. 6. Co-occurrence networks of (a) generalists and specialists, (b) generalists only, (c) specialists only and (d,e) effects of particular lineages on the stability of the networks. Nodes were colored according to different modules. Note the changes in network stability of generalists (d) and specialists (e) when a certain phylum is removed. A connection edge represents a strong (Spearman's $|\mathbf{r}| > 0.6$) and significant (p < 0.05) correlation. The decreasing trend of natural connectivity is fitted with 80% nodes lost, and the R² and slope are shown in diagrams. The lower the absolute value of the slope, the more stable the network

the removal of Chlorophyta, whereas the removal of dinoflagellates and diatoms did not strongly influence the slope, indicating that chlorophytes had a crucial effect on the network stability of the specialists (Fig. 6e).

To test whether the key taxa can have an effect on single-phylum networks, the stability of networks in the presence and absence of dinoflagellates and other phyla in GRL was investigated. In the generalists, the addition of Dinoflagellata to the single-phylum networks of Arthropoda, Bacillariophyta, Chlorophyta and Ciliophora made the networks more connected (Fig. 7a) but degraded network stability, as the declining slopes for these phyla all increased with the addition of dinoflagellates (Fig. 7b). Chlorophyta exhibited a greater influence on specialist cooccurrence patterns than on generalist co-occurrence patterns. In SPL, the addition of Chlorophyta enhanced the network stability of the Arthropoda, Bacillariophyta and Ciliophora single-phylum networks (Fig. 7c,d). In addition, most of the edges in the GRL networks were positive, and the percentage of negative edges increased as dinoflagellates were added to the other phyla. All edges in the SPL networks were positive, indicating the dominance of coexistence instead of exclusion between Chlorophyta and the other phyla.

4. DISCUSSION

4.1. The diversity and drivers of the microeukaryotic community

4.1.1. North—south trend of microeukaryotic diversity consistent with a global-scale latitudinal pattern

An increasing trend was observed in ASV-based diversity along the north—south (i.e. high latitude to low latitude) gradient on the over 3000 km coastline. This is consistent with the latitude-dependent pattern observed over the global ocean (Stehli et al. 1969, Rohde 1992). Several theories have explained why warmer regions support higher biodiversity. Temperature, as an abiotic factor, can control nutrient availability and affect the activity of species, promoting species coexistence (Turner et al. 1987, Clarke & Gaston 2006). Another theory claims that temperature can determine rates of speciation, as temperature can increase metabolic rates through free radicals or reactive oxygen species, which drives mutation rates (Martin 1995, Gillooly et al. 2005). Additionally, the strong climatic

variation at high latitudes requires organisms to have more generalist physiology and ecology (Stevens 1989). By contrast, the weak seasonal variation in climate conditions in lower latitudes can give rise to more localized species ranges; therefore, species richness and diversity will be higher in these areas (Stevens 1989). With higher solar energy availability under higher temperatures, diversity can even be increased through complexification and specialization of biotic interactions such as mutualism, parasitism and trophic interactions (Willig et al. 2003). However, no statistically significant correlation between alpha diversity and temperature was found in this study (Fig. S6). The diversity pattern may be a result of salinity and nutrient concentrations that co-vary with the range of latitudes covered in this study.

The higher diversity within the SS is an exception. Situated in a relatively northern site, the water temperature (annual average: 20.3°C) (Y. Chen et al. 2019) is lower than at the southern study sites (annual average: 22.2°C in XM and 21°C in DS) (Wanjin & Zhaowen 1993, Xu et al. 2023). Thus, temperature cannot explain the higher diversity there. As illustrated in the results, the high diversity in SS may be correlated with PO₄³⁻, as its concentration appears to be distinctly high among the 5 study areas. Evidence exists that variability in phytoplankton diversity can be correlated with phosphorus (Ptacnik et al. 2010). Higher PO_4^{3-} concentration has been linked to higher phytoplankton diversity, which enhances phosphorus use efficiency (Paczkowska et al. 2019). Moreover, studies have shown that the N:P ratios in SS are relatively low (Bu et al. 2024). Generally, the dissolved inorganic nitrogen (DIN; 3.6-61.96 µM) and dissolved inorganic phosphate (DIP; 0.001-1.67 μ M) (Table S1) levels were low in summer compared to the high DIN (39.6–87.5 μ M) and DIP (1.79– $3.77 \mu M$) levels reported in SS in winter (Han et al. 2021). The study also suggests that the exchange of nutrient-poor coastal waters and enhanced biological consumption could lead to relatively low nutrient levels in summer (Han et al. 2021). In addition, the distribution pattern of plankton is likely to be greatly influenced and shaped by aquaculture activities in SS (Li et al. 2024).

4.1.2. Temperature is the primary abiotic factor that drives taxon interactions

In the TINA index (species interaction), the percentage of variance (ADONIS R²) in communities was best explained by temperature (Fig. 3). This result



Fig. 7. Additive impacts of certain phylum interactions on single-phylum networks. (a,b) Generalist and (c,d) specialist changes in network (a,c) topology and (b,d) stability after (a,b) dinoflagellate and (c,d) Chlorophyta interactions (+Dino and +Chlorophyta, respectively) were added to the single phylum networks in the first column of panels. (b,d) The decreasing trend of natural connectivity is fitted with 80% node loss; R² and slope are shown. The lower the absolute value of the slope, the more stable the network

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could be explained by the fact that interactions between heterotrophs and autotrophs or between nonautotrophic taxa (e.g. predators—prey, parasiteshosts) can be influenced by temperature (Traill et al. 2010). To explore how high or low temperatures influenced taxa interactions and network stability, we divided the 5 study areas into 2 groups: a high-temperature group (DS and XM) and a low-temperature group (MJ, PT and SS) (ANOSIM, R > 0). A linear model of removed nodes and natural connectivity was constructed to compare network stability between the 2 groups. The results showed that the network was more stable in the high-temperature group (DS and XM) (Fig. 5b). It is conceivable that temperature can influence the community composition and hence network stability as a result. Temperature alone, or combined with temperature-dependent factors like nutrients, can affect the microeukaryotic community. Positive interactions were also found to be more prevalent with warming (Kordas et al. 2011). Indeed, increased temperature has been shown to have a positive effect on photosynthetic activity (Karlberg & Wulff 2013), productivity and biodiversity of phytoplankton (Yvon-Durocher et al. 2015). Therefore, temperature can modulate species coexistence.

4.2. The ecological processes of microeukaryotic generalists and specialists

4.2.1. Generalists and specialists differ in assembly mechanisms

The lower proportion of generalists and higher proportion of specialists could be due to the environmental heterogeneity among the samples collected (Xu et al. 2022a). A higher abundance of generalists compared to specialists can also result from increased resilience and strategies like higher dormancy potential (Xu et al. 2022a). The specialists appeared to be more likely to be separated into clusters than the generalists (Fig. 2c). Some specialist species were confined to a certain area whereas most generalists were present in all 5 coastal areas (Fig. 2b). Therefore, not surprisingly, specialists have a more distinct spatial pattern. Our results from the null model showed that generalists and specialists differed in assembly processes, and SPL was more shaped by ecological drift (Logares et al. 2018) than GRL (Fig. 4a). According to Logares et al. (2018), ecological drift includes such processes as local adaptation to varying environmental conditions. Therefore, some species in the SPL may have developed adaptations to their local range of environmental conditions such that they are able to tolerate environmental fluctuation in their habitat. In the present study, generalists and specialists were shaped by different selection processes, as generalists were more influenced by homogeneous selection while specialists were more affected by variable selection (Fig. 4a). This

indicates that the community divergence in generalists was constrained by selection and that they were more phylogenetically similar to each other compared to specialists (Logares et al. 2018). Together, this can explain why the GRL and SPL showed disparate spatial patterns. Furthermore, in this study, the richness of generalists was higher than that of specialists. This finding, surprising as it may appear, is consistent with a recent study in which many bacterial generalists and few specialists were present in aquatic environments (Muscarella et al. 2019). Our data showed that the richness of generalists was positively correlated with nutrients (Fig. S6b), suggesting that abundant nutrients may provide support to generalists. A previous study also found that bacterial generalists had advantages in terms of adapting to the environment when resources were sufficient (Egli 2010).

4.2.2. The assembly of microeukaryotic generalist and specialist subcommunities is mainly due to stochastic processes

Despite the distinct assembly mechanisms discussed above, our results revealed that both the generalist and specialist subcommunities were mainly structured by stochastic processes. More specifically, dispersal limitation was the main process for both generalists and specialists (Fig. 4a,b). This is consistent with the ADONIS analysis, which showed that province also contributed greatly to taxon interactions (Fig. 3). The influence of dispersal limitation can also be reflected by geographic distances, as suggested by the Bray-Curtis dissimilarity (Fig. 2b). Stochastic processes have been proven to be more important for shaping the microeukaryotic community than for the bacterial community. Liu et al. (2020) found that in the 23 lakes on the Tibetan Plateau, the microeukaryotic community was strongly driven by dispersal limitation while the bacterial community was triggered by environmental selection. Dispersal limitation was also found to have a larger impact on microeukaryotes in the Tropical North Pacific Ocean (Kong et al. 2022). Similarly, the microeukaryotic community in a subtropical river was strongly driven by stochastic processes (W. Chen et al. 2019). The influence of dispersal limitation was not overestimated for microeukaryotes. First of all, the pattern of DNCI indices suggests a strong dispersal limitation between the community of PT and that of DS and XM (Fig. S10). The water in PT is warm and the most saline of the 5 areas studied here (Fig. S1a,b). The salinity ranged widely in MJ, where DNCI was the lowest among the 5 regions (Fig. S1b), suggesting that the dispersal effect is limited in the estuary where water has a strong gradient of salinity and other factors. Research has suggested that different water masses in different oceans will also have an impact on community assembly (Milke et al. 2022). Therefore, if the water mass had a great influence on dispersal lim-

the water mass had a great influence on dispersal limitation, this is probably because larger cell sizes will enhance the influence of dispersal limitation (De Bie et al. 2012). As a result, larger microeukaryotes would not as easily be moved with currents; thus, their dispersal ability will be relatively weak (Soininen et al. 2011). Bacterial communities were also found to have wider niche breadths (Liu et al. 2020). These findings further support the size-dispersal hypothesis as revealed in many previous studies: larger cell sizes have a stronger dispersal limitation (Foissner 2006, Casteleyn et al. 2010, De Bie et al. 2012, de Vargas et al. 2015). For instance, during the circumglobal 'Tara Oceans' expedition, dispersal limitation was found to increase from piconano- $(0.8-5 \ \mu m)$ to nano- (5- $20 \,\mu\text{m}$), micro- ($20-180 \,\mu\text{m}$) and mesoplankton (180-2000 μ m), as demonstrated in the significantly stronger community differentiation (Mantel test, $R_m = 0.36, 0.49, 0.50$ and 0.51 for the highest piconano- to mesoplankton correlations) by ocean basin in larger organismal size fractions (de Vargas et al. 2015). In this study, we collected organisms that were larger than 3 µm—much larger than most bacteria, which range from $0.22-1 \mu m$. Finally, dormancy strategies are less commonly observed in microeukaryotes than in prokaryotes, and this can contribute to dispersal limitation for microeukaryotes (Wu et al. 2018, Logares et al. 2020). Moreover, microeukaryotic communities of smaller population sizes would also be more influenced by random births and deaths (Wu et al. 2018, Wang et al. 2020).

4.3. The co-occurrence patterns of microeukaryotic generalists and specialists

4.3.1. Different co-occurrence networks in generalists and specialists

Co-occurrence networks are based on ecological associations and taxa interactions within a community (Hirano & Takemoto 2019). The structure and niche spaces shaped by the community members can thus be revealed through co-occurrence patterns (Fuhrman & Steele 2008, Steele et al. 2011, Kara et al. 2013). The co-existence patterns of generalists and specialists are quite different from each other. There were more interaction edges in the SPL network even though there were fewer nodes than in the GRL network (Fig. 6b,c), indicating that the SPL network was more complex. In addition, the generalists interacted more strongly with organisms from the specialists than with each other, and the specialists interacted more strongly with each other than with the generalists (Fig. 6a). This indicates that the specialists are more dynamic than the generalists. Mo et al. (2021) revealed that a more complex network does not always mean more stable co-occurrence patterns. In this study, the more complex SPL network was also found to be less stable than the GRL network (Fig. 6d,e), which further proves the wider distribution of generalists compared to specialists.

There can be several reasons for the different cooccurrence patterns between generalists and specialists. One possible explanation is that more keystone species were identified in the SPL network than in the GRL network (Table S4). According to 2 previous studies, keystone species are generally recognized as the initiating constituents in networks (Barabâsi et al. 2002), and those keystone lineages tend to have a longer evolutionary history (Ma et al. 2016). The networks could break up without these keystone species. As a result, the interactions among taxa may be stronger with more keystone species, and the SPL network was more complex compared to the GRL network. Additionally, the different community compositions of the modules can shape the complexity and stability of co-occurrence networks (Barberán et al. 2012, Mo et al. 2021). In this study, the 2 networks also differed in taxonomic composition and the distribution of species of various phyla or classes. The distribution of specialists was more even across the modules, and different modules were dominated by only 1 or 2 taxa such as Dinoflagellata. In the GRL network, the modules were dominated by several taxa like Dinoflagellata, Chlorophyta, Bacillariophyta and Ciliophora (Fig. S12). We suppose that the dominance of a certain species can contribute to species interactions and network stability. Finally, the percentage of variance in communities explained by different environmental factors (temperature, NH_4^+ and PO_4^{3-}) was also higher for generalists (Fig. 3). The smaller influence of environmental conditions on the SPL as determined by the TINA index might indicate the strong biotic interactions (Y. Wang et al. 2015), which corresponds to the higher number of edges in the specialist co-occurrence network. It is also possible that the SPL is actually more dynamic, and sampling only one time limits the insight it can provide because ecological patterns might be missed (Özkan et al. 2014). 4.3.2. Different determinant taxa for the network stability of generalists and specialists

Recent research in microbial ecology has revealed that rare taxa may be more significant to species interactions (Xiong et al. 2021). In the present study, generalists and specialists differ in the width of the habitat range. Even though generalists are more prevalent than specialists, their taxon interactions are not necessarily stronger. Therefore, the stability of generalists and specialists can be influenced by different taxa.

The change in interaction network stability when a taxon is removed is an indicator of how important this taxon is to stabilizing the network (Tipton et al. 2018). In this study, the removal of dinoflagellates was found to destabilize the GRL network, but not so for the SPL network. This is potentially because dinoflagellates serve as the backbone of the GRL network, which can increase the stability of the entire network (Yang et al. 2022). This finding can be attributed to the contribution made by dinoflagellates to the marine food web. Dinoflagellates are versatile, with diverse trophic modes and high plasticity to environmental variations (Bockstahler & Coats 1993, Jeong 1994, Jeong et al. 2005, Seong et al. 2006). Dinoflagellates interact with a wide variety of marine organisms, and have roles as both predators and prey in the food web (Jeong et al. 2010). Some dinoflagellate predators can graze on chlorophytes (Strom & Buskey 1993), diatoms (Menden-Deuer et al. 2005, Du Yoo et al. 2009), ciliates (Hansen 1991, Bockstahler & Coats 1993) and other dinoflagellates (Tillmann 2004, Adolf et al. 2007); thus, they can control the populations of these prey species. On the other hand, they are the prey of some protistan and metazoan predators, serving as a link between higher and lower trophic levels (Jeong et al. 2010). Therefore, dinoflagellates can enrich the food web complexity and support the co-existence of many microeukaryotic species in the marine ecosystem.

The removal of Chlorophyta had a significant effect on the SPL network, but not on the GRL network. The relative abundance of Chlorophyta in the specialist group was lower than in generalists (Fig. S2b,c). Even if the ecological role of green algae (Chlorophyta) is generally less well-studied than dinoflagellates and diatoms, several studies have indicated their importance (Roger & Reynaud 1982, Sørensen et al. 2014, Tragin et al. 2016). A series of coexistence experiments discovered that the growth of a red tide species, *Prorocentrum micans*, was strongly inhibited by the addition of 2 species of green algae in the form of both fresh tissue and dry powder (Jin et al. 2005). A Chlorophyta– Pyrrophyta–Bacillariophyta type structure was discovered in the overall algal composition of Yuncheng Salt Lake, indicating that Chlorophyta has an advantage in high-salinity waters (Yang et al. 2024). Therefore, green algae, even at low relative abundance, can have a marked effect on the community. Our finding suggests that Chlorophyta deserves further and deeper study. Whereas the addition of dinoflagellates did not increase the stability of single-phylum networks in generalists (Fig. 7a,b), the addition of Chlorophyta did increase the stability of single-phylum networks in specialists (Fig. 7c,d). In contrast to specialists, generalists are typically associated with higher genome sizes and genome expansion (Mas et al. 2016, Xu et al. 2022b), indicating that they are potentially more versatile and less dependent on other organisms in coping with environmental stress. Pandit et al. (2009) postulated that specialists in certain habitats lack environmental plasticity, and hence tend to undergo changes in community composition in response to the fluctuations in environmental conditions. Therefore, community composition can have crucial effects on specialists. Moreover, specialists may depend more on metabolites and other organismal products for growth (Xu et al. 2022b).

5. CONCLUSIONS

Our study investigated the spatial patterns of the microeukaryotic community in 5 coastal areas from south to north in the East China Sea. We found that diversity generally increased from north to south and that microeukaryotic generalists are quite different from their specialist counterparts in terms of spatial distribution, assembly processes, controlling factors and co-occurrence patterns. Our results also indicated that dispersal limitation is the major process shaping the microeukaryotic community structure in the region covered in this study. In addition, Phylum Dinoflagellata, as a major component in the community, has a more important role in community stabilization for generalists than for specialists. Chlorophyta exhibited a major effect on the network stability of specialists but not on that of generalists. Our findings shed light on the underlying mechanisms that shape microeukaryotic generalists and specialists, and enhance our understanding of the significance of species interactions and their potential roles in the microeukaryotic community. As such, this research provides insights into the complex response of plankton to climate and environmental (nutrient, salinity) changes in coastal areas, and can inform biodiversity protection, species conservation and sustainable coastal development.

Data Archive. All 18S rRNA gene sequence data from this study have been submitted to the NCBI database (www. ncbi.nlm.nih.gov/) under accession number SRP466473 and BioProject accession number PRJNA1028181.

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