RESEARCH ARTICLE

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Patterns of bacterial generalists and specialists in lakes and reservoirs along a latitudinal gradient

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Abstract

Aim: The geographical distribution of bacteria is an important, but poorly understood, topic in microbial ecology. A major question is how broadly distributed generalist taxa, and limitedly distributed specialist taxa, vary across a latitudinal gradient in freshwater ecosystems. We predict that: (a) generalists and specialists exhibit latitudinal diversity gradient with different patterns; (b) their community assemblies are mainly driven by stochastic processes; and (c) generalists coexist through niche differences, while specialists coexist through fitness differences.

Location: Sixty lakes and reservoirs in China, ranging from 18° N to 50° N.

Time Period: July–August in 2012 and 2018.

Taxa Studied: Bacterioplankton.

Methods: We clustered zero-radius operational taxonomic unit (zOTU) (subspecies-like level) into operational taxonomic unit (OTU) (species-like level) and calculated the intra-specific variation and spatial asynchrony of OTU. We examined the relative effects of environment versus space (latitude) on bacterial community and quantified the community assembly processes of generalists and specialists, respectively. The binary-state speciation and extinction (BiSSE) model has been used to estimate the evolutionary characteristics. The abundances of the top zOTUs within each OTU were identified to reveal their niche preferences (distribution patterns at different sites).

Results: We found that bacterial generalists had a higher intra-specific variation, greater asynchrony and wider niche width than the specialists. With increasing latitude, bacterial diversity decreased with abundance variations in generalists and occurrence variations in specialists, respectively. Diversification in stochastic processes was the main driving factor in both groups, though deterministic processes showed

greater effects on specialists than generalists in local communities. Bacterial generalists coexisted through niche differences, whereas specialists coexisted through average fitness differences.

Main Conclusions: We demonstrated distinct latitudinal distribution patterns of bacterial generalists and specialists. These results highlight differences in biogeography of microbial generalist and specialist taxa mediated by intra-specific variation and emphasize their distinctly vital roles mediated by differing mechanisms in freshwater ecosystems.

KEYWORDS
bacterial diversity, community assembly, community ecology, intra-specific variation, plankton, species coexistence

1 | INTRODUCTION

Much of ecological theory was developed for large organisms, which leads to the question, to what extent do these ideas apply to microorganisms (Andrews, 2017). Large-scale patterns in the biogeography of macro-organisms are known in great detail, having been studied for several 100 years (Hanson et al., 2012; Mruzek et al., 2022). However, there is currently an ongoing debate over the relative importance of local factors (environmental factors) versus regional factors (spatial factors) in shaping microbial communities, and on whether microbial organisms show a biogeographical signature in their distributions (Aguilar & Sommaruga, 2020; Hanson et al., 2012; Van der Gucht et al., 2007). An historically influential hypothesis developed by Baas-Becking (1934) suggested that – 'everything is everywhere, but the environment selects'. That is, microorganisms are ubiquitous and do not exhibit any specific biogeographical patterns. Instead, they form distinct assemblages shaped by environmental selection. However, increasingly studies suggested that everything is not everywhere and that dispersal limitation also plays a substantial role for global microbial distributions (Fontaneto et al., 2008; Spatharis et al., 2019). Here, we investigate two well-established ecological ideas frequently applied to macroscopic organisms – namely changes in diversity with latitude and the arrangement of organisms along a generalist to specialist continuum. Specifically, we attempt to identify latitudinal variations in the distribution of microbial specialist and generalist taxa.

In freshwater ecosystems, some studies have shown that local environmental factors are predominant in structuring the microbial community (Mazaris et al., 2010; Vanormelingen et al., 2008), while others suggest that both geographical and environmental factors are important (Ju et al., 2014; Soininen et al., 2007). In addition, it has been postulated that the importance of spatial factors increases at larger spatial scales (Soininen, 2012). One aspect that has attracted attention in ecological biogeography is the latitudinal diversity gradient (LDG). A meta-analysis by Hillebrand (2004) with more than 600 latitudinal gradient studies collected from the literature showed that the latitudinal decline in diversity was an ubiquitous phenomenon, but weaker and flatter gradients were observed in freshwater

environments than in marine or terrestrial environments. Clearly latitude itself is part of a human constructed grid pattern, and thus cannot directly affect species richness. However, it is correlated with a wide range of environmental variables, for example temperature, both current and in the geological past, which can result in such effects. Consequently, Sherratt and Wilkinson (2009) argued that latitude was still of use in biogeographical analyses. Ecological theory suggests that, habitat generalists should be abundant and widely distributed, whereas habitat specialists are often rare and of limited distribution (Inceoglu et al., 2015; Macingo et al., 2019; Pandit et al., 2009). If microorganisms have a clear LDG, whether microbial generalists and specialists exhibit distinct biogeographical patterns along latitudinal gradients remains unclear, especially in freshwater ecosystems. Thus, we hypothesize that (i) microbial generalists and specialists exhibit different LDG patterns in freshwater ecosystems.

It has been widely accepted that both deterministic and stochastic processes simultaneously drive the assembly of local communities, but the central question of their relative importance in shaping community composition and biogeography remains open (Sloan et al., 2006; Stegen et al., 2012; Zhou & Ning, 2017). In particular, the contribution of these two ecological processes may differ in community assembly between bacterial generalists and specialists (Lindström & Langenheder, 2012; Székely & Langenheder, 2014). Generalists have a wide habitat preference and appear to respond predominantly to spatial factors, specialists often show a limited distribution and appear to be mostly affected by environmental factors (Logares et al., 2013). While community assembly of bacterial generalists and specialists is well documented, the majority of such studies have focused on soil/sediment or ocean ecosystems (Abdullah AI et al., 2022; Chen, Leung, et al., 2021; Dong et al., 2022; Geng et al., 2022; Logares et al., 2013; Xu, Luo, et al., 2022). In freshwater ecosystems, Liao et al. (2016) reported on differences in bacterial community assembly between bacterial generalists and specialists, but their study was limited to 21 lakes on a single subtropical plateau with monsoon climate (Yungui Plateau, southwestern China). At the large scale, cross-latitude and multi-habitat, environmental heterogeneity might be covered by spatial factors (Soininen, 2012). Thus, the relative importance of stochastic processes controlling aquatic

bacterial generalists and specialists remains unclear in freshwater lakes. We hypothesize that (ii) the community assemblies of microbial generalists and specialists are mainly driven by stochastic processes at a large spatial scale.

Another fundamental question in microbial biogeography is how multiple species can coexist to maintain biodiversity? In contemporary coexistence theory, coexistence mechanisms are classified into either stabilizing or equalizing forces (Chesson, 2000). Thereby, niche differences serve as stabilizing mechanisms that promote species coexistence, whereas average fitness differences are related to equalizing mechanisms that drive competitive exclusion (Chu & Adler, 2015). Rather than debating whether communities are structured by niche or neutral processes, a more informative and important approach concerns the role of niche differences and average fitness differences (Adler et al., 2007; Leibold & McPeek, 2006). Bacterial generalists tend to have a wider niche width and thus better resist environmental filtering, whereas specialists often have a narrower niche width and are likely more sensitive to fluctuating environments (Xu, Luo, et al., 2022). Niche width often – but not invariably – evolves to match the degree of environmental change. Thereafter, specialists evolve in homogeneous and generalists in heterogeneous environments (Kassen, 2002). Yet, generalists and specialists can coexist on a few resources (Birand et al., 2012). Ecologically similar taxa may coexist to a greater degree than expected by chance (Stegen et al., 2012). This raises a fascinating question

about the coexistence of bacterial taxa within generalists or specialists, which – for over 50 years – has been a major issue in ecological theory, where the number of species often appears to exceed the available niches, a phenomenon commonly known as 'The paradox of the plankton' (Hutchinson, 1961). The coexistence of bacterial taxa between generalists and specialists can be influenced by different strategies, such as intra-specific variation, dormancy potential and evolutionary potential (He et al., 2023; Xu, Luo, et al., 2022; Yang et al., 2023). However, bacterial taxa within generalists or specialists have similar ecological strategies, but how they coexist remains unclear. Generalists are normally well adapted to at least one resource and have additional ecological traits that allow them to utilize other resources effectively, while specialists are fairly well adapted to a single, specific resource and utilize other resources inefficiently (Birand et al., 2012). Stronger niche differences lead to equal or weaker competitive interactions between species, while larger differences in average fitness result in greater asymmetry of competitive impacts (Chu & Adler, 2015). Therefore, we hypothesize that (iii) in freshwater ecosystems bacterial generalists show strong niche differences, while specialists greatly differ in their fitness at a large spatial scale.

In this study, we investigated 60 lakes and reservoirs in eastern China ranging from 18° N to 50° N (Figure 1). The size of China results in sampling on a near continental scale, while having the logistical advantage that all the sampling sites are in a single country. We

FIGURE 1 Geographical location of 60 sampling lakes and reservoirs in China. North, high latitude; South, low latitude; EC: electrical conductivity; TSI, trophic state index; WD, water depth. For details of grouping see Table S1.

Group
A: North 1, High EC
B: North 1, Low EC
C: North 2
D: North 3
E: North 4
F: South 1, High TSI
G: South 1, Low TSI
H: South 2, High WD
I: South 2, Middle WD
J: South 2, Low WD
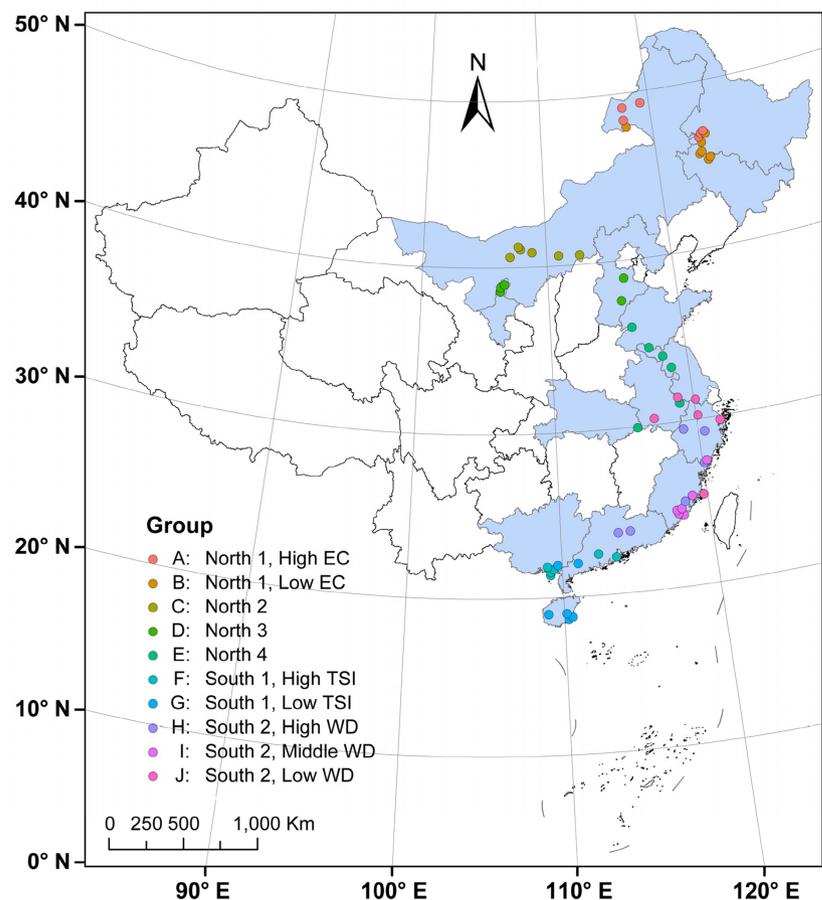
analysed the geographical distribution, community assembly, evolutionary characteristic and species coexistence pattern of bacterial generalists and specialists through 16S rRNA gene Illumina amplicon sequencing. We addressed three major questions: (1) Did bacterial generalists and specialists demonstrate discernible biogeographical patterns across latitudinal gradient? (2) What processes primarily influenced the community assembly of bacterial generalists and specialists? (3) How could bacterial subspecies coexist among generalists or specialists, respectively?

2 | MATERIALS AND METHODS

2.1 | Study lakes and reservoirs

We collected water samples from 60 lakes and reservoirs in eastern China, ranging from 18° N to 50° N (Figure 1 and Table S1). All lakes and reservoirs have been described in our previous studies (Fang et al., 2022; Jin et al., 2022; Liu et al., 2015). Surface water samples were taken at depth of 0.5 m in July and August 2012 (38 waterbodies), and in July and August 2018 (22 waterbodies) (Table S1) at the centre of each waterbody. All samples were kept at 4°C and transported to the laboratory immediately.

2.2 | Physical and chemical analyses

Water temperature (WT), dissolved oxygen (DO), electrical conductivity (EC), pH and turbidity of the waterbody were measured in situ with a multi-parameter water quality analyser (Jin et al., 2022; Liu et al., 2015). Transparency was determined with a 30-cm Secchi disc. Water depth (WD) of each sampling site was detected with a Speedtech SM-5 Depthmate portable sounder (Speedtech Instruments, Great Falls, VA, USA). The concentrations of chlorophyll-*a*, total nitrogen (TN), total phosphorus (TP) and phosphate phosphorus (PO$_4$-P) were measured according to standard methods described in our previous study (Liu et al., 2015). Then trophic state index (TSI) values were calculated based on chlorophyll-*a*, transparency and TP (Yang et al., 2012).

2.3 | DNA extraction and Illumina sequencing

About 500 mL of each water sample was filtered through a 200-μm mesh and then subsequently filtered through 0.22-μm pore size polycarbonate membranes (47-mm diameter, Millipore, Billerica, MA, USA) to collect the bacterioplankton. Membranes with bacterial cells were then stored at −80°C until further DNA extraction. Bacterial DNA was extracted from the membranes using the FastDNA Spin Kit (MP Biomedicals, Solon, OH, USA). For bacterial community analysis, the V3–V4 regions of the 16S rRNA gene were amplified using the primer set 341F and 806R and sequenced with the Illumina NovaSeq platform (Illumina, Inc., San Diego, CA, USA) (Mo, Peng,

et al., 2021). Our PCR reactions had a 20-μL volume in triplicates and consisted of 10 μL Takara Pre-mix Taq (Ex Taq version 2.0 plus dye, Takara Bio, Kusatsu, Shiga, Japan), 0.25 μM of each primer and 10 ng bacterial DNA. All triplicate PCR-amplified products were pooled, purified and quantified for sequencing.

2.4 | Bioinformatics

Amplicon sequencing data were processed using VSEARCH v.2.14.1 (Rognes et al., 2016). Briefly, the forward and reverse reads were merged by MOTHUR v1.39.5 (Schloss et al., 2009) to obtain raw reads. Then, low-quality raw reads were filtered out using 'minuniquesize 8' parameter in VSEARCH for generating unique sequences. Subsequently, the unoise3 algorithm in USEARCH v11 (Edgar, 2010) was used to distinguish zOTUs. The zOTUs were further clustered into OTUs by UCLUST algorithm in USEARCH at a 97% identity threshold. After that, all representative sequences for each OTU were taxonomically assigned against the SILVA database (release 138.1) in USEARCH (Quast et al., 2013). OTU is very similar to species-like level (or species linkage), and zOTU is likely to be subspecies-like (or ecotype) level. To simplify the analysis and description, we term OTUs and zOTUs as species and subspecies respectively – but note that there is a wide range of views to how well the concept of 'species' works for bacterial taxa. All unknown sequences or archaea, chloroplasts, mitochondria and eukaryota sequences in OTUs were discarded. Finally, the whole zOTU dataset was randomly rarefied to 113,007 sequences for each sample and 13,731 zOTU sequences belonging to 5134 different OTUs across 60 samples were retained. All zOTUs in each OTU of every sample were summed generating the OTU dataset. In addition, we also assigned zOTU representative sequences against the SILVA database. On genus level, taxonomies with difference between OTU annotation and zOTU annotation were 894 (6.51% of the all zOTU richness). Among them, 599 divergent taxonomies were generated by annotation resolution, that is to say, sequences were assigned based on OTU, but cannot be assigned based on zOTU, and vice versa. Only 295 divergent taxonomies were directly assigned to different taxonomies. Hence, 97.85% zOTU sequences were assigned into same taxonomies when based on OTU and zOTU.

Intra-specific variation was measured as the natural logarithm of zOTU counts within a taxon at OTU level [ln(zOTU number per OTU)] (Xu, Luo, et al., 2022). Spatial asynchrony of each OTU was calculated based on a previous study (Wilcox et al., 2017) using the modified (Xu, Luo, et al., 2022) formula:

$$\text{asynchrony} = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{N} \sigma_i \right)^2}$$

where σ^2 is the variance in total abundance of OTUs (intra-specific individuals) in each site, σ_i is the spatial standard deviation of abundance of zOTU (intra-specific individual) i within an OTU across N sites (in this study, $N = 60$).

2.5 | Definition of generalists and specialists

The cutoffs for defining bacterial generalists and specialists were somewhat arbitrary (Liao et al., 2016; Mo, Zhang, et al., 2021), we obtained these cutoffs by comparing random and observed OTU level distribution following a recent study (Sriswasdi et al., 2017). If generalists and specialists are considered as two ends of a continuum, then somewhat arbitrary nature of our cutoff likely matches ecological reality. Mantel test showed that latitude, water temperature, WD, EC, transparency and other factors all had a significant effect on bacterial community compositions (Figure S1). However, many lakes or reservoirs in northeast China are alkaline lakes, having higher concentrations of sodium bicarbonate (soda), while in southeast China there are many deep-water or eutrophic reservoirs (higher TSI). Therefore, we divided 10 unique environment groups according to latitude, EC, WD and TSI, to explore the bacterial distribution (Table S1). We also tried constructing groupings (10 unique environment groups) by other factors, such as water temperature and total nitrogen. However, when using ANOSIM (analysis of similarities) to test grouping composition differences, we found the global *R* of groupings based on one factor was low. The global *R* statistic is an indicator of dissimilarities between groups and within groups. An *R* value close to '1' indicates high dissimilarity between groups, whereas an *R* value close to '0' shows an even distribution between groups. After trying groupings with different factors, we found that the global *R* of groupings based on four factors is the highest in groupings based on different (combination) factors (Table S2). Every unique environment group represented a distinctive habitat with specific environmental factors. The OTU dataset was randomly shuffled 10,000 times by keeping the observed OTU richness in each sample to generate a random background distribution. Enrichment of OTUs in most environment groups compared to the random distribution indicates that the OTUs were well able to adapt to their environment groups. These OTUs belong to broadly distributed generalists. In contrast, if the observed OTUs occurred in fewer environment groups than the random distribution, they were defined as specialists with a narrow distribution range. The remaining OTUs that distributed in 2–6 environment groups were classified as opportunists (Figure S2). It should be noted that our classification of generalists and specialists was based on the environment-by-taxa dataset independent of the relative abundance.

2.6 | Functional redundancy index

Functional redundancy index (FRI) analysis can be used to describe the functional profiles of different communities (Beier et al., 2017). 16S rRNA gene sequences of each OTU were used to predict the functions against the database in the 'Tax4Fun2' R packages (R Core Team, 2022) using the 'runRefBlast' command and subsequently FRI was calculated based on the percentages of taxa with a predicted phylogenetic relationship at different Kyoto Encyclopedia of Genes and Genomes (KEGG) levels (Wemheuer et al., 2020).

2.7 | Community assembly processes

The community assembly processes for generalists and specialists were quantified at the OTU level. The 'NST' R package was used to infer determinism and stochasticity in community assembly processes (Ning et al., 2020). Briefly, this method calculates the normalized stochasticity ratio (NST) based on the phylogenetic beta diversity index. It also calculates taxonomic diversities based on the Raup–Crick index (RC value) and the divergences in phylogenetic turnover according to the β nearest taxon index (βNTI) (Stegen et al., 2012). Using the βNTI and RC values, we can infer the relative contributions of five ecological processes, including heterogeneous selection, homogeneous selection, dispersal limitation, homogenizing dispersal and undominated processes (Stegen et al., 2013). The distribution of NST in each environment group and the significance of NST difference between each pair of environment groups were tested by the 'nst.boot' command through bootstrapping for 999 times.

In addition, a neutral community model (NCM) proposed by Sloan was used to measure the relationship between the occurrence frequency of OTU and their relative abundance in meta-communities, which can estimate the potential contribution of stochastic processes in community assembly (Sloan et al., 2006). We also calculated the immigration rate through NCM with R codes following Chen et al. (2019).

2.8 | Evolutionary characteristics of community

The binary-state speciation and extinction (BiSSE) model has been used to estimate the evolutionary characteristics of generalists and specialists (Sriswasdi et al., 2017; Xu, Luo, et al., 2022). In this model, both generalists and specialists were defined as distinct evolutionary states, then evolutionary rate parameters (the speciation and extinction rates as well as the transition rate between generalists and specialists) were estimated. BiSSE was performed with the 'diversitree' R package. The 'starting.point.bisse' function was used to obtain the starting point for the simulation by setting an identical speciation and extinction rate. Then, the maximum likelihood method was used to estimate all rate parameters. At last, a 1000-step Markov chain Monte Carlo (MCMC) simulation was performed to ensure the stability of the final estimate.

2.9 | Statistical analyses

Niche width, refers to the diversity of resources used or environments tolerated by an individual, population, species or clade, was calculated in the 'spaa' R package. Mantel test between bacterial communities and environmental variables was analysed with the 'LinkET' R package to test whether these factors have significant influences on bacterial community composition. Shannon–Wiener index and Chao1 index were calculated using the diversity function

in the 'vegan' R package. Canonical correlation analysis (CCA) was performed in the 'vegan' R package to identify and measure the associations among environmental variables and bacterial community composition. We calculated the Bray–Curtis distance (based on relative abundance) and Sorensen distance (based on presence/absence) in the 'vegan' R package and analysed the distance–decay relationship. All visualizations were performed with the 'ggplot2' R package.

3 | RESULTS

3.1 | Classification of bacterial generalists and specialists

We identified 765 bacterial generalist taxa (OTU existing in more than six environment groups), 2275 bacterial specialist taxa (OTU existing in only one environment group) and 2094 bacterial opportunist taxa (OTU existing in 2–6 environment groups) (Figure S2a). Generalists normally occurred across a wider range of sampling sites with a higher relative abundance, while specialists were restricted to a few sites (Figure S2b). At all sites, the occurrence frequency of generalist taxa was always higher than that of specialists, yet the relative abundance was not. The relative abundance of some specialists at a given site was higher than those of many generalists. This suggests that generalists and specialists exhibited distinct environmental adaptations independent of their abundance.

Bacterial generalists and specialists showed different relationships with environmental factors (Figure S3). CCA showed that generalists clustered together more in space than specialists, and specialists correlated more with latitude, EC, WD and TSI. The pattern in opportunists were similar to the whole community, they

clustered more dispersedly than generalists and more closely than specialists for 10 unique environment groups. This indicates that, in contrast to specialists, the generalists were less controlled by these environmental factors.

More importantly, generalists and specialists showed different intra-specific variations exhibiting differing environmental adaptations (Figure 2). Generalists had significantly higher intra-specific variations than specialists, and opportunists were intermediate (Figure 2a). The detected relationships between niche width and intra-specific variation showed that taxa with higher intra-specific variations had a wider niche width (Figure 2b, $R^2 = 0.35$, $p < 0.001$). We also found that the spatial asynchrony in generalists was much higher than in specialists, while opportunists were intermediate (Figure 2c). Moreover, intra-specific variation and asynchrony exhibited a very strong positive correlation (Figure 2d, $R^2 = 0.69$, $p < 0.001$). Collectively, generalists had a higher intra-specific variation, indicating more ecotypes (zOTUs) within a given OTU. In addition, these zOTUs responded differently to the defined environment groups (higher asynchrony), which resulted in a wider niche width of generalists, implying that they could adapt well to various environments with changing features. In contrast, specialists had a lower intra-specific variation with a lower asynchrony, narrower niche width and they were more sensitive to environmental changes.

3.2 | Latitudinal distribution of bacterial generalists and specialists

Alpha diversity indices of generalists and specialists showed different trends across latitudes (Figure 3). The Shannon–Wiener index (considering relative abundance) of the generalists decreased along
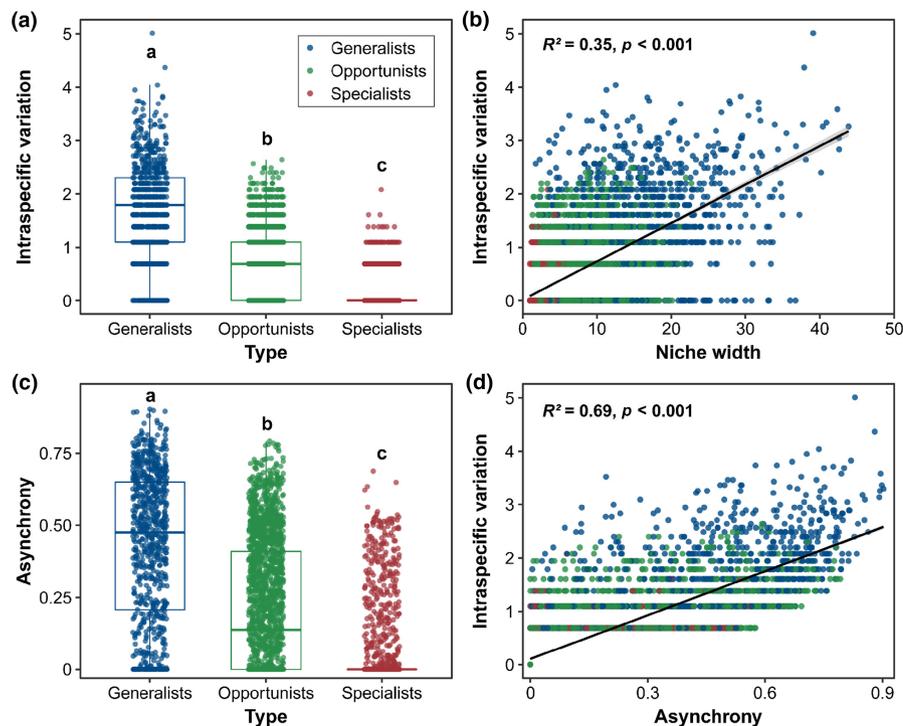
FIGURE 2 Intra-specific variation and spatial asynchrony in bacterial generalists and specialists. Differences of (a) intra-specific variation and (c) asynchrony were examined using analysis of Wilcoxon rank sum tests. Different lowercase letters indicate significant difference between groups ($p < 0.01$). Linear relationships between intra-specific variation and (b) niche width or (d) asynchrony.
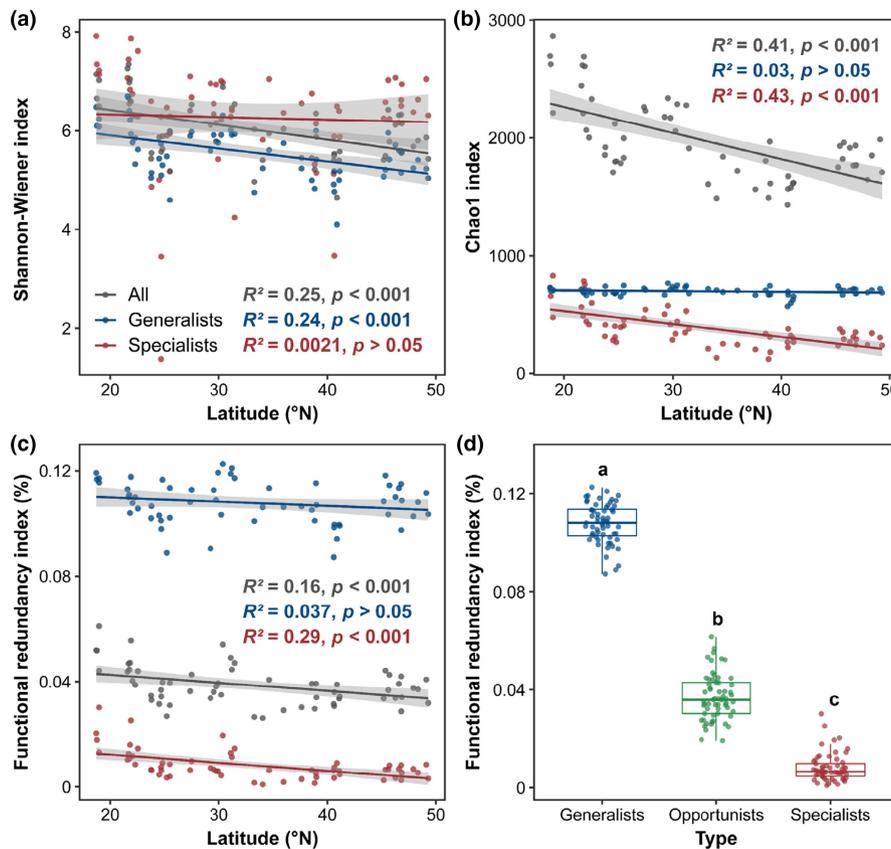
FIGURE 3 Variations in alpha diversity and functional redundancy index (FRI) along latitude. Linear relationships between (a) Shannon–Wiener index, (b) Chao1 index or (c) relative FRI and latitude in the all community, generalists and specialists, respectively. (d) Difference of FRI between generalists, opportunists and specialists based on Wilcoxon rank sum tests. Different lowercase letters indicate significant difference between groups ($p < 0.01$).

latitudinal gradient significantly ($R^2 = 0.24$, $p < 0.001$), whereas the specialists did not show obvious changes ($R^2 = 0.0021$, $p > 0.05$) (Figure 3a). The Chao1 index (taxa richness, considering presence/absence) for the specialists decreased significantly across latitude ($R^2 = 0.43$, $p < 0.001$), whereas the generalists remained unchanged ($R^2 = 0.03$, $p > 0.05$) (Figure 3b). The entire community, however, exhibited a decreasing trend with latitude for both Shannon–Wiener index ($R^2 = 0.25$, $p < 0.001$) and Chao1 index ($R^2 = 0.41$, $p < 0.001$) (Figure 3a,b). In addition, we also compared the linear relationship between Shannon–Wiener index or Chao1 index and TSI or EC, and found that generalists showed similar trends with specialists no matter which diversity index was used (Figure S4). The FRI of the generalists was significantly higher than that of specialists (Figure 3c,d). The FRI of the specialists decreased with increasing latitude significantly ($R^2 = 0.29$, $p < 0.001$), but not for the generalists ($R^2 = 0.037$, $p > 0.05$) (Figure 3c).

There was an apparent distance–decay relationship in both generalists and specialists (Figure S5). Based on Bray–Curtis distance (based on relative abundance), the generalists had a stronger distance–decay in geographical distance ($R^2 = 0.45$, $p < 0.001$) than the specialists ($R^2 = 0.25$, $p < 0.001$) (Figure S5a). The Sorensen distance (based on presence/absence) revealed that the distance–decay relationship of the specialists ($R^2 = 0.29$, $p < 0.001$) was stronger than

that of generalists ($R^2 = 0.17$, $p < 0.001$) (Figure S5b). Moreover, we compared the distance–decay relationships between community similarity and latitudinal distance between the generalists and specialists (Figure S5c,d). Trends in latitudinal distance were the same as for the geographical distance–decay relationships. Based on Bray–Curtis distance, the generalists showed a more pronounced distance–decay (generalists, $R^2 = 0.46$, $p < 0.001$ vs. specialists, $R^2 = 0.26$, $p < 0.001$, Figure S5c), while based on Sorensen distance, the rate was higher for the specialists (generalists, $R^2 = 0.16$, $p < 0.001$ vs. specialists, $R^2 = 0.30$, $p < 0.001$, Figure S5d). Furthermore, we also compared the distance–decay relationships between community similarity and TSI gradient or environmental distance between the generalists and specialists, however, distance–decay relationships were all weaker than those of geographical and latitudinal distance (Figure S6).

3.3 | Community assembly of bacterial generalists and specialists

Based on the NST, community assembly of the bacterial specialists and generalists suggested that generally stochastic processes played a much more important role (88.1% for generalists and 80.1%

for specialists) than deterministic ones (the inner circle in Figure 4). When both selection and dispersal are considered to be undominated processes, community assembly is governed by drift, diversification, weak selection and/or weak dispersal, which is referred to as 'undominated' or simply designated as 'drift'. Thereby, undominated processes were slightly more pronounced in generalists. In addition, the immigration rate of generalists (0.1844), estimated by Sloan's neutral model, was higher than that of specialists (0.0447). There was no obvious dispersal limitation for either generalists or specialists. Deterministic processes were explained by heterogeneous selection for generalists (11.9%) and specialists (18.8%), respectively.

For each of the 10 unique environment groups, the NST of different communities was always >0.5 (Figure S7), indicating that stochastic processes were always predominant within each environment group. For some environment groups, there were significant differences in NST value between environment groups, such as environment group C versus H, C versus I, E versus H and E versus I for generalists and environment group D versus A and D versus F for specialists (the letters A–J refer to the unique environment groups in Table S1 and Figure 1). Yet, NST values between these pairs of environment group were always higher than the average of the medians in the former and later groups within each environment group pair (the dashed line, such as NST between environment group C and environment group H is higher than the average of NST median within environment group C and within environment group H, Figure 5a) of generalists and lower than the average of specialists (Figure 5). Furthermore, we compared the NST values of all environment group pairs (10 environment groups, total 45 environment group pairs). The results show that the majority of NST values between environment group pairs was higher than the average of each environment group pair of the generalists (31 of 45, Figure S8), while most of the NST values between environment group pairs were lower than the

average of each environment group pair of the specialists (27 of 45, Figure S9). These results implied that factors driving generalist community assembly were very similar in the different environment groups, in contrast, specialist community assembly was controlled by specific factors in the different environment groups.

3.4 | Evolutionary characteristics of bacterial generalists and specialists

In our BiSSE model (Figure 6), speciation rate and extinction rate of generalists (18.93 and 2.61) were much higher than those of specialists (0.0010 and 0.0056, respectively). Generalists transition rate (23.40) was 13.9 folds higher compared to specialists (1.68). This suggests that new taxa in generalists are mainly produced through speciation of generalists, while for specialists, new taxa are more dependent on the transition process from generalists to specialists. Distribution patterns of cyanobacterial taxa showed that the common bloom-forming cyanobacteria tended to be composed of both generalists and specialists, while non-bloom-forming cyanobacteria mainly consisted of specialists (Figure S10). This indicates that high transition rate from generalists to specialists leads to generalists containing some specialist variants. It is also worth noting that speciation rate was 7.3 folds higher than the extinction rate for generalists, while the extinction rate was 5.6 folds the speciation rate of specialists, implying that both generalists and specialists showed a strong diversification at community level, but the underlying drivers might be different at large spatial scale.

3.5 | Species niche preferences of bacterial generalists and specialists

The top six most abundant OTUs (based on relative abundance) and their constituent zOTUs (i.e. the two top zOTUs of each OTU in terms of relative abundance) in generalists and specialists were selected as representative results to explore their cumulative abundances at the different sampling sites (Figure 7). The two constituent zOTUs of a given generalist OTU occurred at the majority of all sampling sites, but showed a complementary distribution and most of their abundance peaks were complementary (Figure 7a). For example, in OTU3 (*Cyanobium* sp.), zOTU31 occurred at the left part and zOTU9 at the right part of the sampling sites (Figure 7a). Thus, the combination of zOTU31 and zOTU9 resulted in the existence of OTU3 across most of the studied sites. In contrast, the two constituent zOTUs in a given specialist occurred at the similar sites (Figure 7b), for example, in OTU1108 (unassigned Sphingomonadaceae), zOTU14027 and zOTU14033 always co-occurred at the same sampling sites.

To verify the niche preferences (distribution patterns at different sites) of zOTUs, we selected more OTUs and calculated the z-scored abundances of the top 20 zOTUs within each OTU, irrespective of their abundance. Niche preferences of zOTUs within the top 20 generalist OTUs revealed that zOTUs exhibited different niche
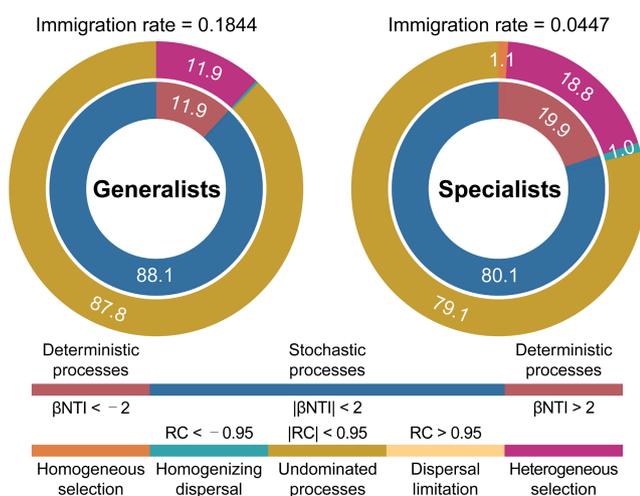
FIGURE 4 Community assembly of bacterial specialists and generalists. The inner circle indicates the contribution of stochastic and deterministic processes to bacterial community assembly. The outer circle shows the percentage of different ecological processes. For simplicity, explained percentages <1% are not shown.

FIGURE 5 Boxplot showing the normalized stochasticity ratio (NST) of generalists or specialists within or between environment groups. Single letter represented NST within this environment group, while groups with 'vs.' indicated that NST between the former and latter environment group (i.e. 'C vs. H' shows NST between environment group C and environment group H; see Figure 1 for different environment groups). The dashed line represents average of median in former environment group and latter environment group. Only environment groups with significant differences are shown (for details see Figure S7).
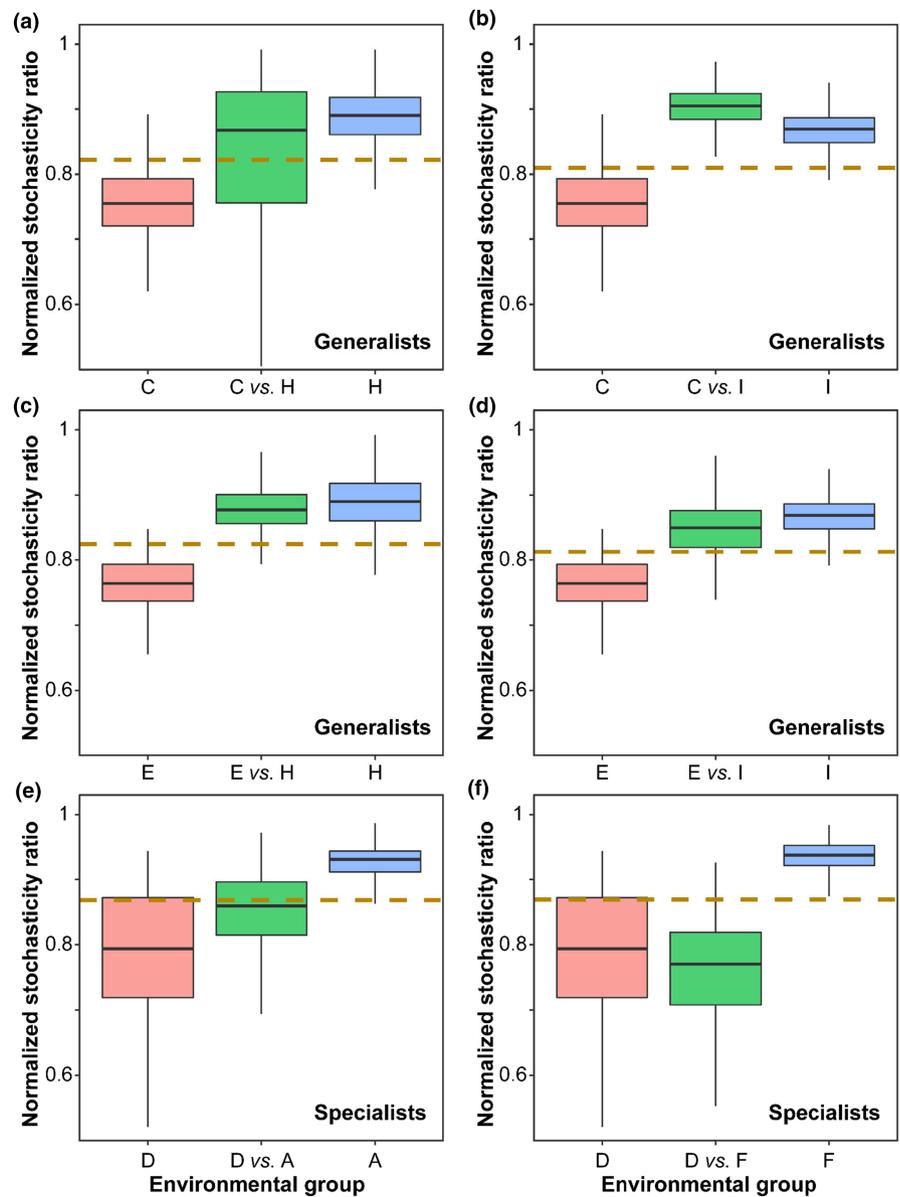
preferences, resulting in a wide geographical distribution of the generalist OTUs (Figure S11). On the contrary, zOTUs within the top 20 specialist OTUs only occurred at a limited number of sampling sites and showed a very similar niche preference (Figure S12). Overall, zOTUs of generalists had different niche preferences indicating a high degree of niche width for the respective generalist OTUs, while those of specialists exhibited similar niche preferences, indicating a low niche width of the respective specialist OTUs.

4 | DISCUSSION

Our study has three major results: (1) bacterial generalists showed a LDG with variations in abundance, while specialists exhibited variations in occurrence (absent/present); (2) stochastic processes were the main driving factors in both bacterial generalists and specialists; (3) generalists coexisted by stabilizing mechanisms through niche

differentiation, whereas specialists coexisted by equalizing mechanisms through average fitness differentiation.

4.1 | Latitudinal distribution patterns of bacterial generalists and specialists

Although biogeographical patterns are crucial for understanding ecology, the distinction between generalists or specialists is often neglected (Villalba et al., 2022) when trying to predict and explain spatial distribution patterns of microbial biodiversity (Xu, Vandenkoornhuyse, et al., 2022). In our study, bacterial diversity and community similarity exhibited variations in generalists and specialists with increasing latitude (Figures 3a,b and S5). A study based on 40 shallow lakes in the Yangtze-Huaihe River basin showed that generalists, rather than specialists, mainly contributed to the variation in beta diversity across the trophic gradients (Geng et al., 2022).
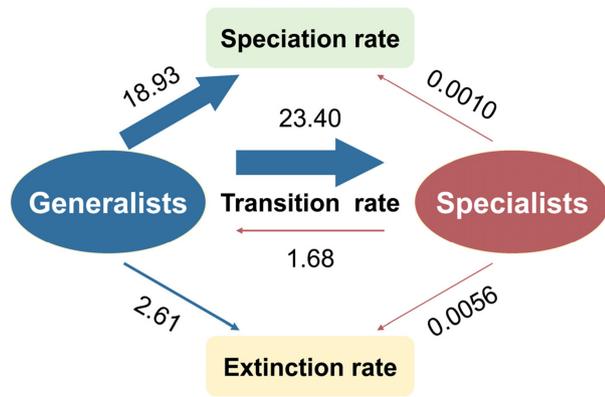
FIGURE 6 Estimation of evolutionary characteristics for generalists and specialists based on the binary-state speciation and extinction (BiSSE) model. The thickness of the arrows represents the magnitude of the rate, while the number means the corresponding value.

However, we found that both generalists and specialists were important and contributed to the variations in community diversity and similarity in different aspects. Variations in alpha and beta diversity across the latitudinal gradient were higher, or more significant, than those variations across trophic gradients or other environmental distance. In addition, for generalists the FRI did not change significantly with increasing latitude, while for specialists or the entire bacterial community it did (Figure 3c). This implies that the specialists might disproportionately contribute to the FRI of the entire bacterial community, suggesting that specialist diversity is highly relevant for ecosystem functions. Microbial metagenome-assembled genomes (MAGs) from Arctic seawater also revealed the vital role of specialists for global biogeochemical cycles as all KEGG-annotated generalist genes were found in specialists, whereas 814 specialist genes were not detected in any generalist MAG (Royo-Llonch et al., 2021).
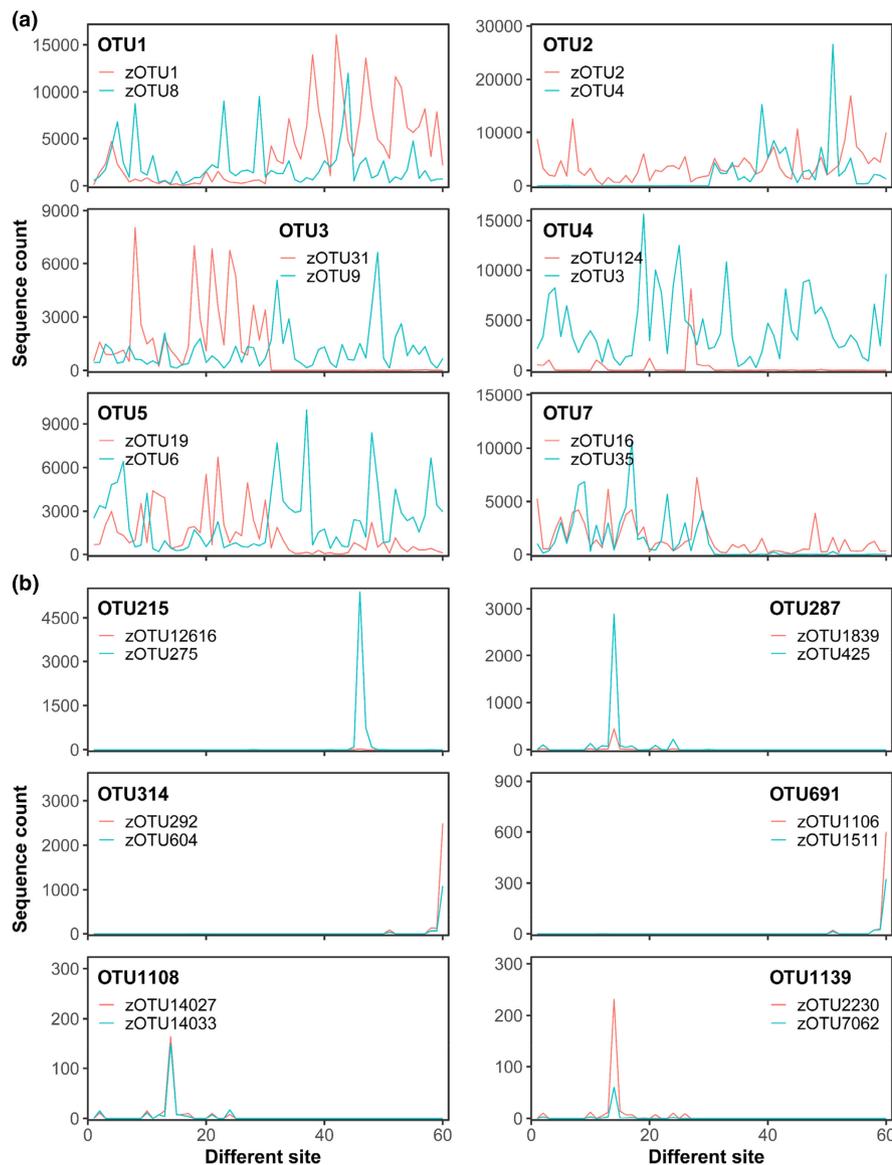
FIGURE 7 Distribution of zOTUs within the (a) generalist or (b) specialist groups, respectively. Different colours represent the different constituent zOTUs of generalists or specialists. The six most abundant generalist and specialist OTUs and two most abundant zOTUs within each OTU are shown.

4.2 | Community assembly processes of bacterial generalists versus specialists

Generally, generalists show better adaptation to environmental changes than specialists and their community assembly processes are mainly driven by stochastic processes. In contrast, specialists are more sensitive to environmental changes and their assembly processes are dominated by deterministic processes that is evolution of 20 budding yeast populations in 11 laboratories (Jerison et al., 2020), rainwater bacteria in microcosms (Langenheder & Székely, 2011), bacteria and fungi in water and sediments of shallow lakes (Geng et al., 2022), bacteria in farmland soil (Xu, Vandenkoornhuyse, et al., 2022), freshwater cable bacteria in river sediment (Dong et al., 2022) and bacteria in Yungui Plateau lakes (Liao et al., 2016). Indeed, in this study, specialists were more controlled by environmental selection than generalists (Figure 4). Conclusively, immigration rate of generalists was much higher than specialists, leading to an efficient adaptation to different environmental conditions. Interestingly, in both bacterial taxa, stochastic processes were more dominant than deterministic ones (Figures 4 and S7). Previously, this has been also found for bacterial generalists and specialists of sediment bacteria of various Tibetan lakes (Yan et al., 2022). However, in farmland soil, generalists were dominated by stochastic processes, while specialists were driven mainly by deterministic processes (Xu, Luo, et al., 2022; Xu, Vandenkoornhuyse, et al., 2022). This divergency can be explained by differences in dispersal between soil and water habitats that is in aquatic ecosystems, dispersal limitation and environmental heterogeneity might be low compared to soils. In our study, dispersal limitation was not detected at all and homogenizing dispersal was very low for both generalists and specialists (Figure 4). Moreover, undominated processes in stochastic processes contributed substantially to community assembly of both generalists and specialists, as there was high diversification (Figures 4 and 6), which implied that diversification played a vital role in aquatic community assembly (Hanson et al., 2012; Milke et al., 2022; Ning et al., 2020). A recent study in the Pacific Ocean illustrated that drift (undominated process) can be of major importance for both particle-associated and free-living prokaryotic communities in the upper mesopelagic waters (Milke et al., 2022). In the Yungui Plateau lakes, though bacterial generalists were driven by neutral or stochastic processes, only 50.9% of the community variation could be explained by the neutral model (Liao et al., 2016). In addition, Liao's study was limited to the subtropical monsoon climate, different from our study which covered highly diverse climate zones from tropical to subtropical and to temperate regions (Table S1). A previous microcosm study revealed that generalists mainly assemble stochastically, while species sorting occurs more often among specialists (Langenheder & Székely, 2011). This experiment is very distinct from our field study as in microcosms the initial assembly of bacterial communities differs from that of the more established complex and, thus, stable assemblies in natural environments. Consequently, in more open and stable aquatic

bacterial communities, stochastic processes might be dominant in both generalists and specialists, but specialists would be affected more by deterministic processes in less stable environments.

The NST results confirmed these findings and revealed that stochastic processes were more prominent than deterministic processes no matter which bacterial community (entire, generalist and specialist) was considered (Figure S7). Interestingly, when environment group pairs were considered, the NST values between the environment group pairs tended to increase in generalists (Figures 5a–d and S8), but decreased in specialists (Figures 5e,f and S9). This suggests that the driving factors for generalists in different environment groups are very similar, independent of environmental changes. Specialists, however, seem to be highly dependent on environmental changes as they are driven by numerous distinct factors. Many studies showed that environmental factors (i.e. lake trophic status or physico-chemical variables) and spatial factors (i.e. latitude, longitude, geographical distance) are both important in shaping microbial communities and their biogeographical distributions (Barberán & Casamayor, 2010; Crump et al., 2007; Ferrera et al., 2017; Jin et al., 2022; Schiaffino et al., 2011). Moreover, the relative contribution of environmental factors and spatial factors shaping lake meta-communities across floodplain systems seems to be scale dependent and environmental factors predominant at the local scale, while the relative importance of spatial factors seems to increase at the large spatial scale (Lansac-Tôha et al., 2020). In our study, we found that both generalists and specialists showed a clear geographical distribution along the latitude (Figures 3 and S5), rather than environmental factors (Figures S4 and S6), indicating the vital roles of spatial factors for shaping bacterial communities at the larger scale. At the same time, environmental factors contributed more to the community assembly of specialists than generalists (Figures S3, S8 and S9), implying that the community compositions of specialists were more strongly influenced by local environmental factors. In 20 urban waterbodies, bacterial and micro-eukaryotic specialists were more influenced by the habitat type (i.e. water and sediment) than pollution level (Abdullah Al et al., 2022). This is in agreement with our study where specialists responded to numerous environmental factors rather than a single factor such as pollution level. At a regional scale, however, both generalists and specialists seem to be strongly affected by geographical factors, whereas at the local scale, environmental factors seem to have a stronger effect on specialists than generalists.

4.3 | Species coexistence mechanisms in bacterial generalists and specialists

Evolutionary characteristics of generalists and specialists indicate a model of microbial dispersal driven by the ability of generalist taxa to expand across different environments (Sriswasdi et al., 2017). Speciation rate and extinction rate of generalists were much higher than those of specialists (Figure 6), which is contrary to what has been observed for macro-organisms as conservation biology literature

suggests that generally, specialists are more prone to extinction than generalists in natural ecosystems at population level (Hambler & Canney, 2013). Generalists showed higher speciation rates than extinction rates, whereas specialists showed the opposite pattern (Figure 6). Thereafter, generalist taxa emerge and spread into different environments, experience distinct evolutionary pressure and many of them evolve into new taxa well adapted to their new habitats. Specialists become extinct when environments change dramatically, but can recover from taxa transition from generalists to specialists at community level. The generalist–specialist evolutionary cycle implies that microbial diversity is maintained more through continual replenishments of specialists from generalist taxa than through persistence of specialist taxa in natural ecosystems (MacLean, 2005; Sriswasdi et al., 2017). This highlights a key role of generalists in microbial dispersal and evolution of specialization. However, it is important to notice that there might be some limitations with the results from our BiSSE model. Speciation and extinction are typically examined across phylogenies with as many taxa from each clade as possible. When compared to global eDNA data of freshwater bacteria (Tessler et al., 2017), though we did not include all known taxa in lakes globally, bacteria identified from our 60 lakes and reservoirs would very likely cover the majority of bacteria in any relevant environment. Besides, the 'diversitree' R package used to run our BiSSE model provides a method to randomly include taxa or represent taxa in 'unresolved clades' in cases where not all extant taxa are included in a phylogenetic clade (FitzJohn, 2012). High taxa coverage and random-sampling of taxa in the 'diversitree' might give us some effective predictions about the occurrence of taxa occurring in specific regions.

Aquatic microbial generalist and specialist taxa both have high diversification rates with opposite evolutionary routes. It has often been argued that evolutionary diversification is the result of divergent natural selection for specialization on alternative resources (MacLean, 2005). Further, it is suggested that specialists hold greater diversification rates because they are more likely to suffer from resource limitation and, thus, are more susceptible to environmental changes (Xu, Luo, et al., 2022). Other researchers have an opposite view that is generalists have higher diversification rates because they are more widely distributed, resulting in higher rates of allopatric speciation based on a higher likelihood to encounter ecological or geographical barriers (Rolland & Salamin, 2016; Xu, Luo, et al., 2022). Our findings are partly inconsistent with the above views. Net diversification rate refers to the difference between speciation and extinction rates (Rolland & Salamin, 2016). Our work supports key findings from previous studies demonstrating that both speciation and extinction rates of generalists are always higher than those of specialists at community level (Sriswasdi et al., 2017). However, differences between speciation and extinction rates were higher in our study than soil microorganisms (Sriswasdi et al., 2017). In aquatic ecosystems, microorganisms can spread easily, hence generalists with strong environmental adaptations can easily invade into new environments and form new permanent populations, while specialists sensitive to environmental changes are more likely to vanish when faced with various serious environmental stress. Across micro- and macro-organisms or different habitats, specialist taxa with narrower habitat ranges and greater reliance on specific resources are more likely to get extinct at population level (Birand et al., 2012; Sriswasdi et al., 2017).

Generalist and specialist taxa are distinct in their evolutionary characteristics and niche preferences. Consequently, generalist taxa might mainly coexist through niche differences and adaptation to multiple environments, whereas specialist taxa tend to coexist through average fitness differences by maximizing their fitness in a specific optimum habitat (Rain-Franco et al., 2022). For example, the specialist *Microthrix parvicella* adopt fitness trade-offs rather than accumulated genetic variations when facing fluctuating environmental conditions (Muller et al., 2014). Moreover, when microbial populations comprise high frequency of generalists, they also tend to contain various specialists, each belonging to a different environment (Birand et al., 2012; Sriswasdi et al., 2017). In our study, we found that *Dolichospermum* (formerly *Anabaena*), *Planktothrix*, *Aphanizomenon*, *Raphidiopsis* (formerly *Cylindrospermopsis*) and *Microcystis* comprised not only some generalists, but also contained some specialists with relatively wide geographical distributions (Figure S10). Therefore, these harmful or bloom-forming cyanobacterial taxa do not only extend their niche width to access more resources, but also improve their fitness via a more effective resource exploitation. Generalist and specialist cyanobacteria often adopt different strategies, which can be described by two hypotheses that is the Red and Black Queen hypotheses (Strotz et al., 2018). The latest comparative genomic studies revealed that cyanobacteria have a high phenotypic plasticity, habitat adaptation and fitness advantages over other phytoplankton in various environments (Chen, Teng, et al., 2021; Willis & Woodhouse, 2020). For example, filamentous freshwater cyanobacteria have a widespread capability to use phosphonates, that is they can use methylphosphonate as an alternative phosphorous source when inorganic phosphorus and organic phosphoesters are depleted (Zhao et al., 2022). This also implies that filamentous cyanobacteria have great advantages in oligotrophic and mesotrophic deep lakes or reservoirs where inorganic and organic phosphorus is often limited as phosphonates can be used as an alternative phosphorus source. Consequently, researchers and government managements need to carefully evaluate the risks of cyanobacterial blooms in deep lakes and reservoirs as they are able to access additional nutrient resources.

5 | CONCLUSIONS

We demonstrated distinct latitudinal distribution patterns of bacterial generalists and specialists based on 60 lakes and reservoirs in eastern China. We found that not only generalist abundance, but also specialist occurrence strongly responded to latitudinal changes. At the regional scale, both of them were affected by geographical factors; whereas at the local scale, environmental factors exhibited stronger effects on bacterial specialists than generalists.

Diversification in stochastic processes was the most important factor driving generalist and specialist community assemblies. Thereby, evolutionary characteristics suggest that generalists play key roles in generating new taxa and maintaining taxa diversity in aquatic bacterial populations. Higher intra-specific variation and spatial asynchrony of generalist taxa introduced by different niche preferences lead to species coexistence through niche differences. In contrast, specialist taxa are more likely to coexist through average fitness differences. Our work highlights the exceptional role of stochastic processes in aquatic microbial community assembly and reveals the influence of intra-specific variation on distribution and coexistence patterns of generalist versus specialist taxa along the latitudinal gradient. Therefore, ecological management and cyanobacterial bloom prevention need differential strategies to deal with microbial generalists and specialists in inland waters.

AUTHOR CONTRIBUTIONS

Jun Yang conceived the idea and designed the research. Lemian Liu, Peng Xiao and Huihuang Chen collected the samples. Jun Zuo and Zijie Xu performed the experiments. Jun Zuo analysed the data. Jun Zuo, Jun Yang, David M. Wilkinson and Hans-Peter Grossart wrote the first draft of the manuscript, and all authors contributed to revisions and approved the final version of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw sequence data were submitted to NCBI (the National Center for Biotechnology Information, https://www.ncbi.nlm.nih.gov/) under the BioProject accession number PRJNA694227. Code is available at https://github.com/Johnny-zuo/BISSE.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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