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The scale-dependence of spatial distribution of reservoir plankton communities in subtropical and tropical China

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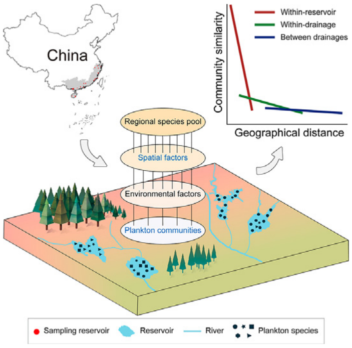
HIGHLIGHTS

- Distance-decay relationships (DDRs) are well-established patterns in ecology.
- Both phytoplankton and zooplankton were studied in 24 reservoirs from 13 drainages.
- The DDR patterns of both plankton communities were spatial scale-dependence.
- The slopes of DDR patterns decreased with the magnification of spatial extent.
- The plankton communities were shaped by environmental and spatial processes.
- Dispersal was a more dominant assembly process than niche-based processes.

GRAPHICAL ABSTRACT

A conceptual paradigm showing distance decay relationships at different spatial scales (within-reservoir, within-drainage but between reservoirs, and between drainages) in 24 reservoirs in subtropical and tropical China. The geometric symbols represent plankton species, while the blue region indicates reservoir.



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ABSTRACT

Distance-decay relationships (DDRs) represent a very useful approach to describing the spatial distribution of biological communities. However, plankton DDR patterns and community assembly mechanisms are still poorly understood at different spatial scales in reservoir ecosystems. We collected phytoplankton, zooplankton and water samples in 24 reservoirs from subtropical and tropical China from July to August 2018. We examined DDR patterns across three distinct spatial scales, i.e., within-reservoir, within-drainage (but between reservoirs) and between drainages. We tested whether the rate of change (i.e., slope) of DDRs is consistent across different spatial scales. We assessed the relative importance of spatial and environmental variables in shaping the community distribution of plankton and quantitatively distinguished the community assembly mechanisms. We observed significant DDR curves in phytoplankton and zooplankton communities, in which slopes of the DDRs were steepest at the smallest spatial scale. Both spatial and environmental factors had significant impacts on DDR and dispersal assembly was a slightly stronger process in reservoir phytoplankton and zooplankton community assembly than niche-based process. We conclude that DDRs of reservoir phytoplankton and zooplankton vary with spatial scale. Our data shed light on how spatial and environmental variables contribute to plankton community assembly together. However, we revealed that dispersal process contributes to the biogeography of reservoir plankton slightly more strongly than environmental filtering. Collectively, this study enhances the understanding of plankton biogeography and distribution at multiple spatial scales.

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1. Introduction

Beta diversity (i.e., variation in species composition between communities) is an essential concept in characterizing the change or species turnover of community composition across space and time (Legendre et al., 2005). Distance-decay relationships (DDRs) are the most well-established biogeographical patterns in describing species spatial turnover in ecology, which describes how the similarity in species composition varied along with the geographical distance between communities (Morlon et al., 2008; Anderson et al., 2011). DDR curves depict the beta-diversity (i.e., community similarities) of the community against distance, and their slopes can be used to assess the rate of turnover in space from site to site (Soininen et al., 2011).

Major part of the knowledge on distance-decay relationships originates from macroorganisms, while the spatial distribution of plankton communities have received attention only in very recent years (Soininen et al., 2011; Astorga et al., 2012; Zhang et al., 2018; Chen et al., 2019). Clear distance-decay gradients have been observed across various communities and a variety of spatial scales (Martiny et al., 2011; Bahram et al., 2013; Gao et al., 2019; Zhao et al., 2019). So far, however, there is still a lack of research on the DDR patterns of reservoir phytoplankton and zooplankton communities, although studies suggested that some plankton groups exhibit distinct spatial distribution patterns in streams, oceans or connected lakes within a single watershed, based on data originating from both microscopic and molecular approaches (Soininen et al., 2011; Astorga et al., 2012; Kent et al., 2016; Zhang et al., 2018; Chen et al., 2019). Hence, a relevant question remains whether plankton communities show similar DDR patterns at various spatial scales as seen in soil bacteria communities (Martiny et al., 2011; Gao et al., 2019) and soil fungal community (Zhao et al., 2019).

Community assembly has been studied from different perspectives, where empirical evidence shows that several processes and mechanisms influenced community establishment. Some distance-decay studies have focused on species dispersal process and environmental filtering as underlying drivers behind the patterns (Astorga et al., 2012; Zhang et al., 2018). It is known that community assembly of aquatic microbial communities comprises both deterministic and stochastic processes (Xue et al., 2018; Chen et al., 2019). Plankton plays an important role in primary production (Elser et al., 2000; Harpole et al., 2011) and energy transfer to higher trophic levels (Bellier et al., 2014) in aquatic ecosystems, and it is, therefore, necessary to understand the biogeographical patterns and community assembly mechanisms of plankton in inland waters (Soininen et al., 2005; Isabwe et al., 2018; Lansac-Toha et al., 2019). A full understanding of plankton community dynamics also requires the explanatory data on environmental, hydrological, and biological aspects (Isabwe et al., 2022; Yang et al., 2017).

Some studies observed that the community assembly of plankton was influenced by different biotic and abiotic drivers ranging from the local scale to the continental scale (Soininen et al., 2011; Bellier et al., 2014; Izaguirre et al., 2016). With this type of complexity, there is a need for field observations that test the roles of different processes and mechanisms of plankton community assembly across different spatial scales. The actual processes driving phytoplankton and zooplankton communities include mass effects, species sorting, dispersal limitation (Bortolini et al., 2017) and ecological heterogeneity among species (Bellier et al., 2014). Mass effect is important in a homogeneous environment at small spatial scales; but with the increase in spatial scale and environmental heterogeneity, the role of species sorting increases (Cottenie, 2005). Species sorting by niche differentiation proved that heterogeneity in environmental factors and the species interactions caused by abiotic factors can shape local communities (Leibold et al., 2004). Nevertheless, spatial processes related to dispersal limitation may also be important in shaping phytoplankton community (Soininen et al., 2011; Verreydt et al., 2012). Neutral processes (i.e., stochastic dispersal and ecological drift) can also influence community assembly, which states that all species are functionally equivalent while drift is the primary driver of community composition (Hubbell, 2005).

The role of spatial processes in determining plankton community assembly across different spatial scales is still largely unclear. Some studies suggested that dispersal limitation increases with spatial distance (Soininen et al., 2011; Verreydt et al., 2012; Heino et al., 2015). However, as the importance of these processes on plankton community varies with spatial scale, DDR is also likely to vary so that mass effect is probably dominant at a smaller scale while dispersal limitation dominates at larger scales (Bortolini et al., 2017). It is thus necessary to characterize the drivers underlying the community assembly from local to a larger scales to fully understand the biogeography of plankton.

Here we ask the following questions: (1) are DDR patterns of plankton communities scale-invariant? (2) To what extent do spatial or environmental variables explain the DDR patterns of plankton communities and do the balance of underlying drivers vary with phytoplankton and zooplankton? (3) What are the major mechanisms that maintain the community assembly of reservoir plankton in subtropical and tropical China?

2. Materials and methods

2.1. Study sites and sampling

In total, 24 reservoirs with different nutrient levels in 13 drainages were sampled in five provinces (Zhejiang, Fujian, Guangdong, Guangxi and Hainan provinces) in subtropical and tropical China during July and August 2018 (Fig. 1). These reservoirs covered a wide nutrient and climatic range, characterized by a subtropical and tropical monsoon climate. The surface area of the reservoirs ranges from 0.84 to 595.00 km^2 and the water depth of sampling sites varied between 1.0 and 75.3 m (Wang et al., 2022). The drainage system information of the studied reservoirs is presented in Table S1. Almost all of the reservoirs are for water resource supply and energy generation. Macrophytes are rare in the deep reservoirs perhaps due to the water level fluctuation.

To detect the species occurring in the reservoirs as well as possible, at least three sites were sampled in each reservoir, except for Shikang Reservoir in which only one site was sampled due to major difficulties in accessing the reservoir. The representative sampling sites of each of the reservoirs were selected from the upstream of the reservoir region to the front of the dam. Totally, 106 surface samples were collected from these 24 reservoirs.

2.2. Plankton collection and identification

Plankton samples were collected by a 5-L polymethyl methacrylate sampler at 0.5 m below the water surface. Phytoplankton samples (2.5 L) were stored in bottles and fixed with 1.5 % Lugol's iodine solution (Lv et al., 2014). Phytoplankton samples were identified to species level with an inverted microscope. For small number of species that cannot be accurately identified to specific species, we used sp. to distinguish them at the genus level. Quantitative phytoplankton analysis was completed using microscopy following the method described by Yang et al. (2017). A minimum of 500 units (single cell, colony, and filament) was counted in each phytoplankton sample (Zhang and Huang, 1991; Hu and Wei, 2006). The taxonomy and nomenclature information of phytoplankton was updated based on the AlgaeBase (https:// www.algaebase.org). The biovolumes were estimated using a geometric shape for each taxon unit (Hillebrand, 1999). Biovolumes of phytoplankton were estimated based on the provided geometric shapes and mathematical equations. Phytoplankton biomass (mg/L) was estimated through their biovolumes (Lv et al., 2014). We approximate the density of phytoplankton to the density of water. Biomass equals 1 mg/L multiplied by the biovolumes.

Zooplankton samples (30 L) were filtered through a 64-μm pore-size net and preserved with formaldehyde in the field (Chen et al., 2021). The zooplankton were identified and counted with an inverted microscope. At least

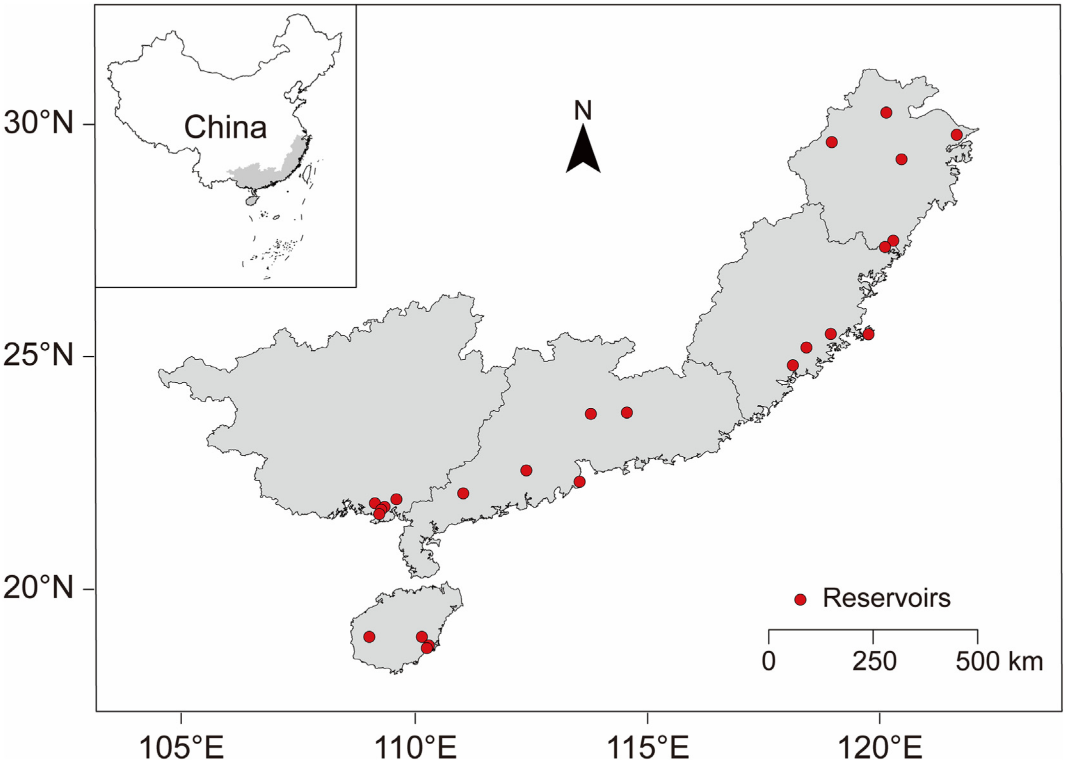

Fig. 1. The 24 studied reservoirs in five provinces in subtropical and tropical China. The surface water and plankton samples were collected from July to August in 2018.

300 individuals per sample were counted (Zhang and Huang, 1991; Soininen et al., 2011). Zooplankton biomass (mg/L) was estimated through their biovolumes (Baranyi et al., 2002). The estimation of zooplankton biovolume and biomass was similar to that of phytoplankton.

2.3. Physical and chemical analysis

Water temperature (°C), pH, dissolved oxygen (mg/L), turbidity (NTU), electrical conductivity (μS/cm), salinity, oxidation-reduction potential (ORP) (mV) were recorded *in situ* with a multi-parameter water quality analyzer (Hydrolab DS5, Hach Company, Loveland, CO, USA). Transparency was estimated with a 30-cm diameter Secchi disk. Filters for chlorophyll-*a* (Chl-*a*) (μg/L) were frozen until analyses, which were filtered by glass fiber filters (GF/F) after recording the volumes of water (Zhang et al., 2018). The extraction of Chl-*a* was performed in acetone and measured by the spectrophotometric method. Unfiltered samples were collected in a polypropylene flask to measure the concentrations of total carbon (TC) (mg/L), total nitrogen (TN) (mg/L), and total phosphorus (TP) (mg/L). Samples for measurement of total organic carbon (TOC) (mg/L), ammonium nitrogen (NH_4-N) (mg/L), nitrate nitrogen (NO_3-N) (mg/L), nitrite nitrogen (NO_2-N) (mg/L), phosphate phosphorus (PO_4-P) (mg/L) were stored in polypropylene bottles after filtration (GF/F, 25 mm diameter, 0.7 μm mesh), and measured with the standard method (Yang et al., 2017). The TOC-VCPH (Total Organic Carbon Analyzer, Shimadzu Corporation, Japan) was used to measure total carbon (TC) and total organic carbon (TOC). Total nitrogen (TN) (Alkaline potassium persulfate digestion UV spectrophotometry method), ammonium nitrogen (NH_4-N) (Nessier's reagent spectrophotometry), nitrate nitrogen (NO_3-N) (Ultraviolet spectrophotometry), nitrite nitrogen (NO_2-N) (N-(1-naphthyl)-1,2-diaminoethane dihydrochloride spectrophotometry), total phosphorus (TP) and phosphate phosphorus (PO_4-P) (Ammonium molybdate spectrophotometric method) were measured by spectrophotometry method. The comprehensive trophic state index (TSIc) was calculated based on chlorophyll-*a*, transparency and total phosphorus following a previous study (Yang et al., 2012).

2.4. Catchment-level data

Landscape images were downloaded from a data-sharing infrastructure of earth system science in China (http://www.geodata.cn/). The catchment or drainage boundaries and reservoir boundaries were delineated by the digital elevation model (DEM) in ArcGis 10.6 software (ESRI, Redlands, CA, USA). The catchment area and reservoir area data in the summer of 2018 were extracted from Landsat 8 images. The drainage and reservoir landscape images were converted into raster images. The catchment area (CA) and reservoir area (RA) were estimated based on the raster images in ArcGis 10.6 software. The ratio of catchment area to reservoir area (CA/RA) was then calculated for each reservoir, respectively. The environmental factors and drainage variables data of the studied reservoirs are presented in Table S2.

2.5. Statistical analyses

The map of sampled reservoirs was created by the "maptools" package (Bivand and Lewin-Koh, 2020) in the R software version 3.6.1 (R Core Team, 2019). To characterize the beta-diversity of phytoplankton and zooplankton communities, community similarities were determined by Bray-Curtis matrices based on biomass data.

To explore if the DDR patterns of plankton communities were scale-invariant, we first investigated the relationships between phytoplankton/zooplankton community similarities and log-transformed geographical distance at different spatial scales. Distance decay relationships were computed for each sampling site and divided into three spatial scales (within-reservoir, within-drainage but between reservoirs, and between drainages) based on if the pairwise sampling sites were from the same reservoir or drainage (catchment). Sampling sites within drainage included that in the same drainage but between reservoirs. The relationship curves were calculated using the "vegan" package (Oksanen et al., 2016) and visualized with the "ggplot2" package (Wickham, 2016). The slopes of DDR curves were calculated using a linear least squares regression (using the log-transformed geographical distance) on the relationships between phytoplankton or zooplankton community similarity and geographical distance in km (Martiny et al., 2011). To ensure that our results were not biased by the dataset size, we explored a random selection in the largest sub-dataset (between drainages, sample size: 4869) with the smallest dataset size (within-reservoir, sample size: 215) based on phytoplankton and zooplankton biomass data, respectively. The random selections were conducted 20 times for dataset sizes from 200 to 4800 every 200 intervals and the Spearman rank correlation coefficient and P values were calculated.

Variation partitioning analysis (VPA) was used to assess the importance of spatial and environmental factors on phytoplankton or zooplankton community variations based on redundancy analysis (RDA), respectively (Peres-Neto et al., 2006). The phytoplankton and zooplankton data were Hellinger-transformed, and the environmental parameters were $\log(x + 1)$-transformed except for pH, to improve normality and homoscedasticity before statistical analyses. For RDA, spatial factors were calculated from geographical distances through principal coordinates analysis of neighbor matrices (PCNM). The spatial factors (PCNMs) were determined using the pcnm function in "vegan" package. Variables with variance inflation factors (VIFs) below 10 were kept in the analysis to reduce multicollinearity among spatial factors and environmental factors.

To tease apart the relative importance of geographical distance and environmental factors on phytoplankton and zooplankton communities, a multiple regression on matrices (MRM) approach was used (Martiny et al., 2011). As a forward selection, variable clustering was carried out to assess the environmental variables redundancy. Using the VARCLUS procedure in the "Hmisc" package (https://hbiostat.ort/R/Hmisc/), only the variables with lower correlation (Spearman $\rho^2 < 0.7$) were kept in the MRM model (Martiny et al., 2011). We removed chlorophyll-*a* from the MRM analyses on the phytoplankton community, but kept it for zooplankton community. All significant factors were kept for the analyses of phytoplankton and zooplankton communities, respectively.

To evaluate the importance of different processes on the phytoplankton and zooplankton communities, we modeled the direct and indirect effects of spatial processes, catchment-level processes, and local processes on phytoplankton/zooplankton communities using the structural equation modeling (SEM) (Liu et al., 2019). Factors from different scales represented corresponding influence processes. All factors were $\log(x + 1)$-transformed except for pH, following variation partitioning analysis. The SEM is a multivariate approach to test the causal hypotheses against data. To evaluate the effect of each factor, we constructed a SEM to examine the direct and indirect effects of spatial and environmental variables on phytoplankton/zooplankton community. The initial model included all plausible paths between phytoplankton/zooplankton community composition, spatial, physical, and chemical variables. Non-metric multidimensional scaling (NMDS) ordination was used to summarize the variation in the distribution of the phytoplankton/zooplankton community (NMDS axes 1 and 2) with the PRIMER 7.0 (PRIMER-E, Plymouth, United Kingdom) (Clarke and Gorley, 2015). The correlations between physical and chemical variables were not included to reduce the complexity of the SEM models, and only significant pathways ($P < 0.05$) were retained in a stepwise method. Improved model fit was evaluated by the reduced χ^2 and Akaike information criterion. The overall fitness of the final SEM model was assessed by the goodness-of-fit index (GFI), Bentler comparative fit index (CFI), and χ^2 test. The SEM analysis was performed using the "lavaan" package (Mamet et al., 2019).

Finally, to disentangle the relative importance of dispersal and niche processes in shaping plankton community assembly, dispersal-niche continuum index (DNCI) values were calculated in the 'DNCImper' package (Vilmi et al., 2020). The DNCI provides a quantified measure of the main assembly processes based on presence/absence data. Positive and negative values of DNCI indicate that niche-based or dispersal-based process dominates community assembly, respectively. All analyses to assess processes and mechanisms that maintain plankton community assembly were conducted on a combined spatial scale perspective.

3. Results

3.1. Plankton community composition

A total of 305 phytoplankton species and 89 zooplankton species were identified in 106 samples from 24 studied reservoirs. All phytoplankton species belonged to eight groups (Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanophyta, Euglenophyta, Pyrrophyta, and Xanthophyta). The phytoplankton biomass ranged from 1.63 ± 0.35 mg/L (mean ± s.e.) in Xinfengjiang Reservoir to 65.01 ± 11.83 mg/L in Nanxi Reservoir. Bacillariophyta, Chlorophyta and Cyanophyta dominated the phytoplankton biomass in most cases, while Pyrrophyta species dominated in some reservoirs (Fig. S1). All identified zooplankton taxa belonged to Cladocera, Copepod or Rotifer. The maximum value of zooplankton biomass was recorded in the Sanshiliujiaohu Reservoir (1.25 ± 0.41 mg/L), and the minimum zooplankton biomass was observed in the Qiaodun Reservoir (0.07 ± 0.01 mg/L) (Fig. S2). The species lists of phytoplankton and zooplankton are provided in the supplementary information (Table S3 and Table S4).

3.2. Spatial scale-dependence of plankton beta-diversity

Across all spatial scales, phytoplankton and zooplankton community similarities decreased significantly with geographical distance based on Bray-Curtis similarity ($P < 0.01$, Fig. 2). However, there were important differences in the slopes of distance-decay relationships (DDRs) among the three spatial scales. At the within-reservoir scale, the DDR slope was steepest, while the slope became shallower and the correlation became weaker with increasing the spatial scale (within-drainage but between reservoirs or between drainages) (Fig. 2). Furthermore, DDR pattern of the zooplankton community was different from that of the phytoplankton community at within-drainage (but between reservoirs) scale (Fig. 2).

Distance decay was also achieved significance separately for three of the dominant phytoplankton phyla (i.e., Bacillariophyta, Chlorophyta and Cyanophyta) within a reservoir, yet phytoplankton communities were overall weakly spatially structured across drainages (Fig. S3). There were notable differences in DDR patterns for non-dominant groups (Chrysophyta, Cryptophyta, Euglenophyta, Pyrrophyta, and Xanthophyta), as they did not show any significant DDR within a reservoir or drainage (Fig. S3). The rates of DDR patterns in community similarity were highest among the different zooplankton groups (Cladocera, Copepod and Rotifer) within reservoir (Fig. S4). The results of our random sub-sampling indicated that these findings are reliable and provide evidence that the significant DDRs were not derived from the sample size effect because 98 % of randomly selected data were significant (Fig. S5).

3.3. Variables associated with plankton community assembly

According to variation partitioning analysis (VPA), spatial factors always remained effective in explaining community composition and exhibited a stronger effect on phytoplankton communities than environmental factors (Fig. 3). The VPA results also showed that spatial factors significantly explained more zooplankton community variation than environmental factors (Fig. 3). When VPA was run on different groups, spatial factors had higher explained variation than environmental factors, except for rotifer (Fig. 3).

In MRM analyses, we observed that geographical distance contributed the largest partial regression coefficients on phytoplankton ($b = -0.257$, $P < 0.001$) and zooplankton ($b = -0.147$, $P < 0.001$) communities (Table S5). However, the varying importance of geographical distance and environmental factors reflected the difference in underlying variability for different phytoplankton and zooplankton groups, respectively (Table S5). In general, the explanation of phytoplankton community changes by geographical distance was better than that of the zooplankton community (Table S5).

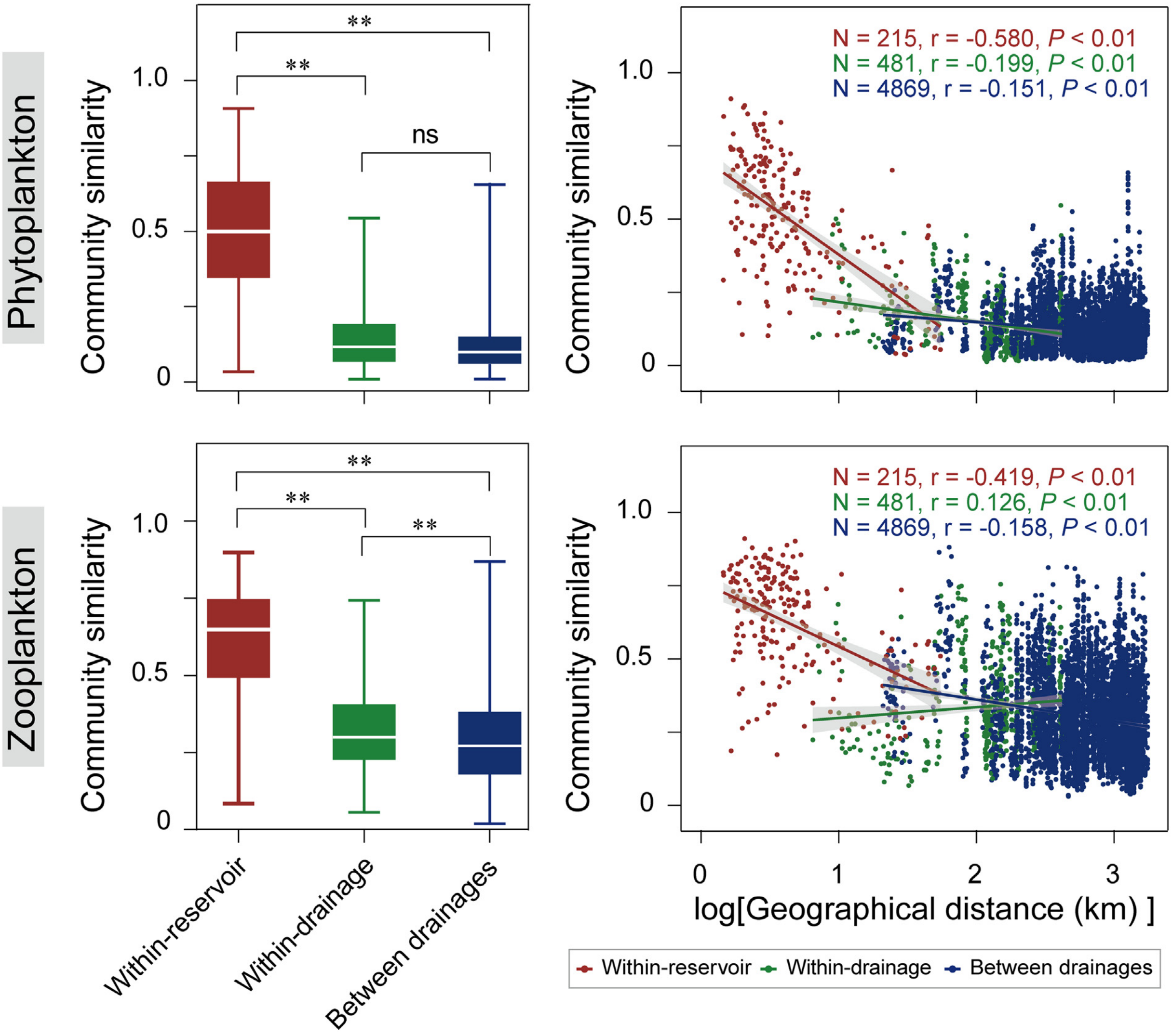

Fig. 2. Distance decay relationships based on the Bray-Curtis similarity of plankton community and log-transformed geographical distance at three scales (within reservoir, within drainage but between reservoirs, and between drainages). Significant differences (**, $P < 0.01$; ns, $P \geq 0.05$; Wilcoxon rank-sum test) between the three scales are indicated by asterisks. Boxes and error bars indicate the 25th/75th and 5th/95th percentiles, respectively; middle line of the boxes is the median. The shaded area around the lines covers 95 % confidence.

We then used structural equation modeling (SEM) to explore the potential direct and indirect impacts of spatial, catchment-level and local processes on plankton community composition (Fig. 4, Fig. 5). The 70 % and 76 % variations of phytoplankton NMDS axes 1 and 2 were explained by three scale-related environmental variables, respectively. Variables between drainages (spatial variables) affected the phytoplankton community directly and by influencing variables of the other scales indirectly (Fig. 4). Variables within drainage (but between reservoirs) only contributed to variables within reservoir. Variables of the within-reservoir scale had strong and significant effects on the phytoplankton community (Fig. 4). The zooplankton community variation (NMDS axis 1: 46 %; NMDS axis 2: 53 %) was less explained than that of the phytoplankton community. Nevertheless, factors within drainage (but between reservoirs) had a direct effect on zooplankton community variation (Fig. 5).

The DNCI values of plankton communities were slightly lower than 0, indicating that dispersal assembly was a slightly more important process for the phytoplankton and zooplankton communities than the niche-based process (Fig. 6). Only in a few sampling sites niche related process was a more important process that drove plankton community assembly.

4. Discussion

Our analyses indicated that: (i) there were significant DDR patterns in plankton communities at three spatial scales in most cases, but the slopes decreased with the increase in spatial scale from local to regional scales; (ii) our study provides strong evidence that spatial and drainage-level (catchment-level) variables influenced plankton community distribution by impacting environmental factors within reservoir; (iii) dispersal process and environmental filtering are important for plankton assembly, but dispersal process plays a slightly more prominent role between reservoirs.

4.1. The scale-dependence of distance-decay patterns in plankton communities

Various studies have suggested that significant DDRs emerge in plankton communities (Soininen et al., 2011; Wetzel et al., 2012; Zhang et al., 2018), although there are notable exceptions to this (Beisner et al., 2006; Nabout et al., 2009). Our findings that the DDRs were significant in plankton communities agree with previous studies for stream diatoms and river phytoplankton (Astorga et al., 2012; Wetzel et al., 2012), lake plankton in different boreal drainage systems (Soininen et al., 2011), and phytoplankton communities in different seasons (Zhang et al., 2018). Even if

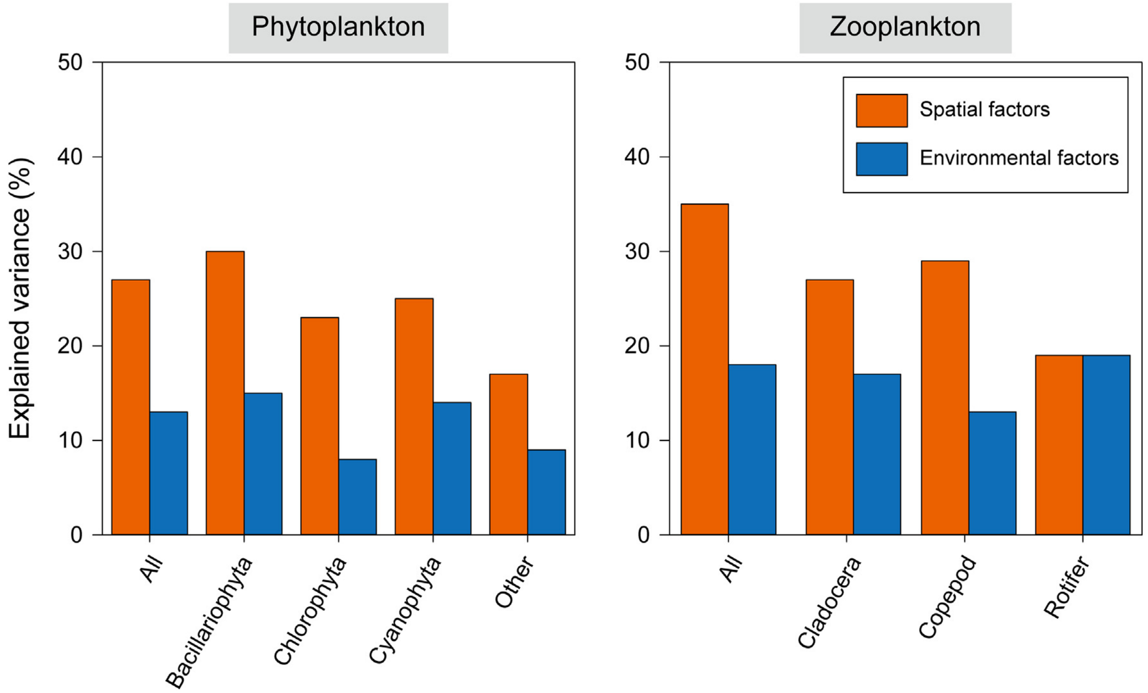

Fig. 3. Proportions of reservoir plankton community variation explained by spatial factors (orange) and environmental factors (blue) based on phytoplankton and zooplankton biomass, respectively.

significant DDRs seem to be more common in plankton, some exceptions to this deserves also to be mentioned. In shallow lakes of the Yangtze River watershed in China, the significant DDR in phytoplankton communities was only found at a small spatial scale (< 12 km) in summer, whereas it was non-significant at multiple spatial scales in spring (Zhang et al., 2018). The difference in DDR patterns between spring and summer stemmed from two main reasons. First, the beta diversity of phytoplankton in summer was greater than that in spring. Second, the spatially structured environmental factors increased spatial community dissimilarity by altering species composition from spring to summer (Zhang et al., 2018).

More importantly, our most notable finding was that the slopes of DDR became flatter with increasing spatial scale for plankton communities and their subgroups. This meets the prediction of Soininen et al. (Soininen et al., 2011) that the halving distance (i.e., the distance that halves the community similarity) is shorter (i.e., and thus DDR slope is steeper) for smaller study scales. This result indicates that the community similarity of plankton decreases rapidly with geographical distance especially within reservoir, differing from the recent studies on other domains, where the slopes of DDRs were flat at the within habitat scale (Martiny et al., 2011; Zhao et al., 2019). We further found that the slope of DDRs was significantly shallower at the within-drainage (but between reservoirs) scale than that of within-reservoir scale. Such finding concurs with several lake bacterioplankton, lake zooplankton, reservoir diatom and freshwater phytoplankton studies that show a comparably mild slope across larger spatial scales (Nelson et al., 2009; Bellier et al., 2014; Mazaris et al., 2010; Marquardt et al., 2018). These consistent results demonstrate that community similarity first decreases rapidly to low level with increasing spatial scale, after which the community similarity does not decrease with the expanding spatial scale.

The absolute values of the correlation coefficient of DDR were largest within reservoirs in most cases, which indicates the strongest explanatory power of the DDR models. A similar finding of the highest explanatory power at the within-reservoir scale agrees with a stream diatom study in Finland in which the strongest DDRs were found at the scale of <200 km (Astorga et al., 2012). Together, such results indicate that the relationships between plankton community similarities and geographical distance are perhaps stronger at the smaller spatial scale.

Several reasons may account for the scale-dependence of DDRs of plankton communities within reservoirs. First, the within-reservoir scale was relatively large (< 1 km to 53 km) when compared with plankton individuals (ranging from several micrometers to several millimeters), and we found that environmental heterogeneity increased steadily with spatial scale also within reservoirs (Fig. S6). In addition, the environmental heterogeneity at the regional scale (between drainages) was significantly larger than that at the local scale (within-reservoir). Second, initial community similarities were high in adjacent sampling stations from the same waterbody, which typically leads to strong distance decay (Soininen et al., 2011). Third, dispersal rates can strongly mediate the compositional response of plankton communities (Verreydt et al., 2012). The zooplankton community composition and grazing rates were affected by the increased dispersal rates, which can mediate the changes in community composition at a lower trophic level (such as phytoplankton and bacterioplankton) (Verreydt et al., 2012). In small reservoirs, plankton species with high dispersal rates aggregate mainly through mass effect (Lindstrom and Langenheder, 2012), which explains their high initial community similarity as the mass effect can rescue plankton species from local extinction. Compared with smaller ecosystems, in large reservoirs, the distances are too large for plankton to disperse effectively, thus reducing mass effects.

4.2. Major role of spatial variables in shaping plankton community

Disentangling the effects of spatial and environmental variables has been a major challenge in microbial ecology (Yang et al., 2012; Liu et al., 2015; Jiao et al., 2020). High environmental heterogeneity and the decrease of community similarity along spatial distance were found within reservoir and within drainage (but between reservoirs), which indicates the spatial factors affect community composition together with environmental factors. PCNM is a method to produce a series of decompositions of spatial relationships among sampling sites, based on diagonalization of a spatial weighted matrix (Bellier et al., 2007). The stronger effect of spatial factors in shaping the plankton communities was confirmed by the VPA result. This

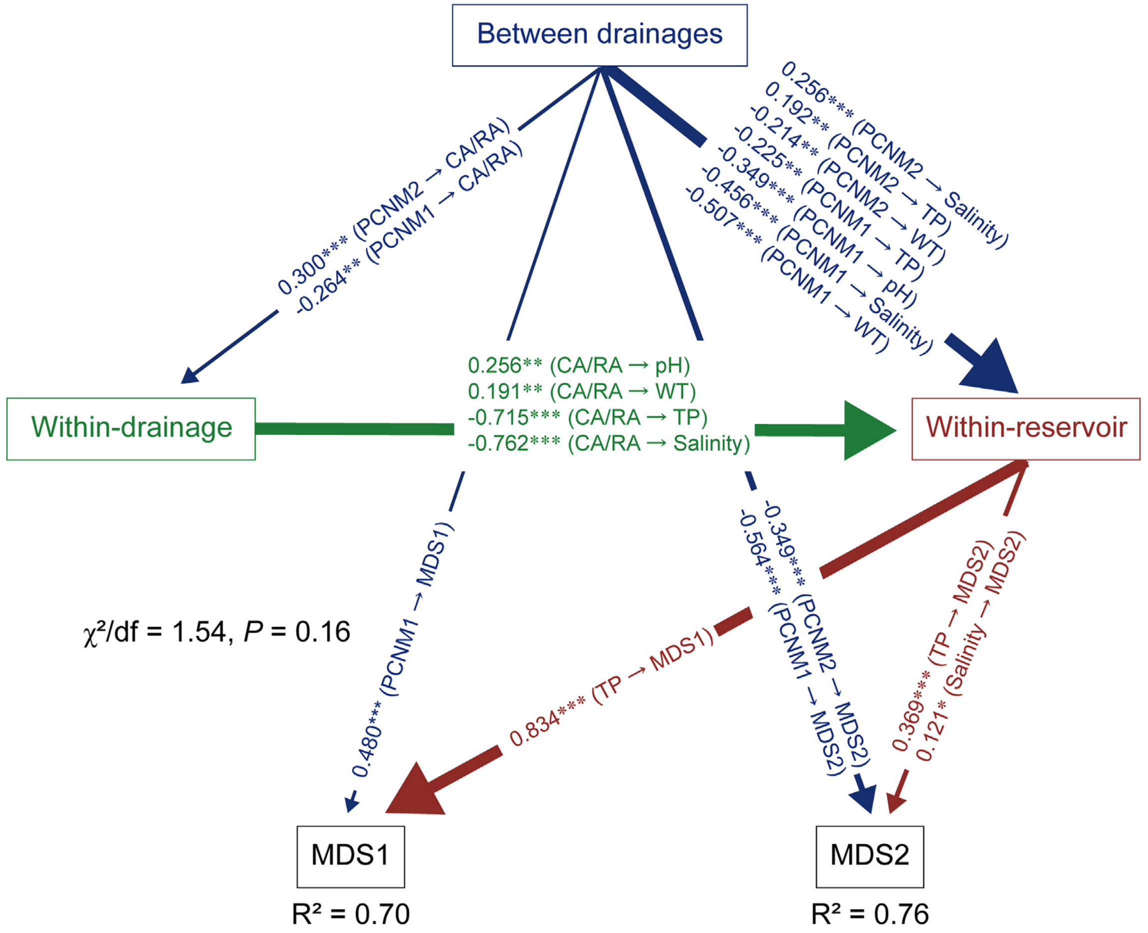

Fig. 4. Structural equation model (SEM) analysis showing the relationships between the spatial factors, environmental factors and the first two axes of phytoplankton non-metric multidimensional scaling (NMDS) ordination based on 106 samples from 24 reservoirs in subtropical and tropical China. SEM co-variates are colored by corresponding scale (blue represents between drainages factors, green represents within drainage but between reservoirs factors, and brown represents within reservoir factors). Numbers near each arrow indicate partial correlation coefficients associated with each causal relationship, and arrow thickness is proportional to the sum of absolute values of the partial correlation value. The GFI (0.991), CFI (0.993), and $\chi^2/\mathrm{df} = 1.54$, $P = 0.16$) adjusted model indicated that the model was good fit to the original data.

finding was in line with a previous study of the lake phytoplankton communities of the Yangtze River watershed in China (Zhang et al., 2018).

The MRM analyses revealed that both geographical distance and environmental factors contribute to the spatial patterns of the plankton communities and illustrated the largest contribution of geographical distance for all phytoplankton and zooplankton, respectively. However, in general, the variability in community similarities of some groups of phytoplankton and zooplankton emphasized the role of environmental factors. This organization of scale-dependence was also suggested by theoretical studies (Gonzalez et al., 2020). The complexity of biodiversity (taxonomic diversity, functional diversity and their effective numbers), biotic associations and species interactions (food webs or interactive networks) may cause various organizational scale-dependence in results (Gonzalez et al., 2020). The organizational scales align with spatial or temporal scales in the importance of research on community ecology.

To predict the complex and dynamic changes in the phytoplankton and zooplankton communities, we further built SEM to link community composition and biotic or abiotic variables to ecological processes. These results indicated that variation of the plankton communities was mainly driven by spatially structured environmental heterogeneity and dispersal process. To be specific, the phytoplankton and zooplankton community distributions were mainly affected directly by environmental factors within-reservoir. The spatial factors (the PCNMs between drainages) indirectly affected phytoplankton and zooplankton community distributions by influencing the local environmental factors. These results indicated that the regional scale factors were more likely to impact the local scale factors, and thus changed the plankton community distribution. However, we cannot totally rule out the possible importance of unmeasured abiotic (e.g. heavy metals and climatic effect) and biotic variables (i.e., competition and grazing), which might account for some of the observed differences in plankton communities (Yang et al., 2017; Gao et al., 2021). Our VPA result showed equal effects of spatial and environmental factors on rotifer community distribution. The difference between rotifer and other plankton groups may be caused by biotic interactions. Rotifers and crustacean plankton are known to compete for many same food resources, and rotifers can be interfered with by larger cladocerans (Baranyi et al., 2002).

4.3. Mechanisms underpinning plankton community assembly

According to our VPA and SEM results, both spatial and environmental factors were proven to shape the plankton community distribution. Thus, dispersal process and species sorting were the main community assembly mechanisms of phytoplankton and zooplankton communities. We showed that dispersal process can have manifold consequences in shaping the plankton community compositional similarity at multiple spatial scales, as indicated by (weakly) negative DNCI values in plankton communities between reservoirs (Fig. 6). In a meta-analysis of aquatic ecosystems, dispersal process was found to be the main shaping mechanism of plankton community assembly (phytoplankton and zooplankton) (de Bie et al., 2012). Passive dispersal enables species

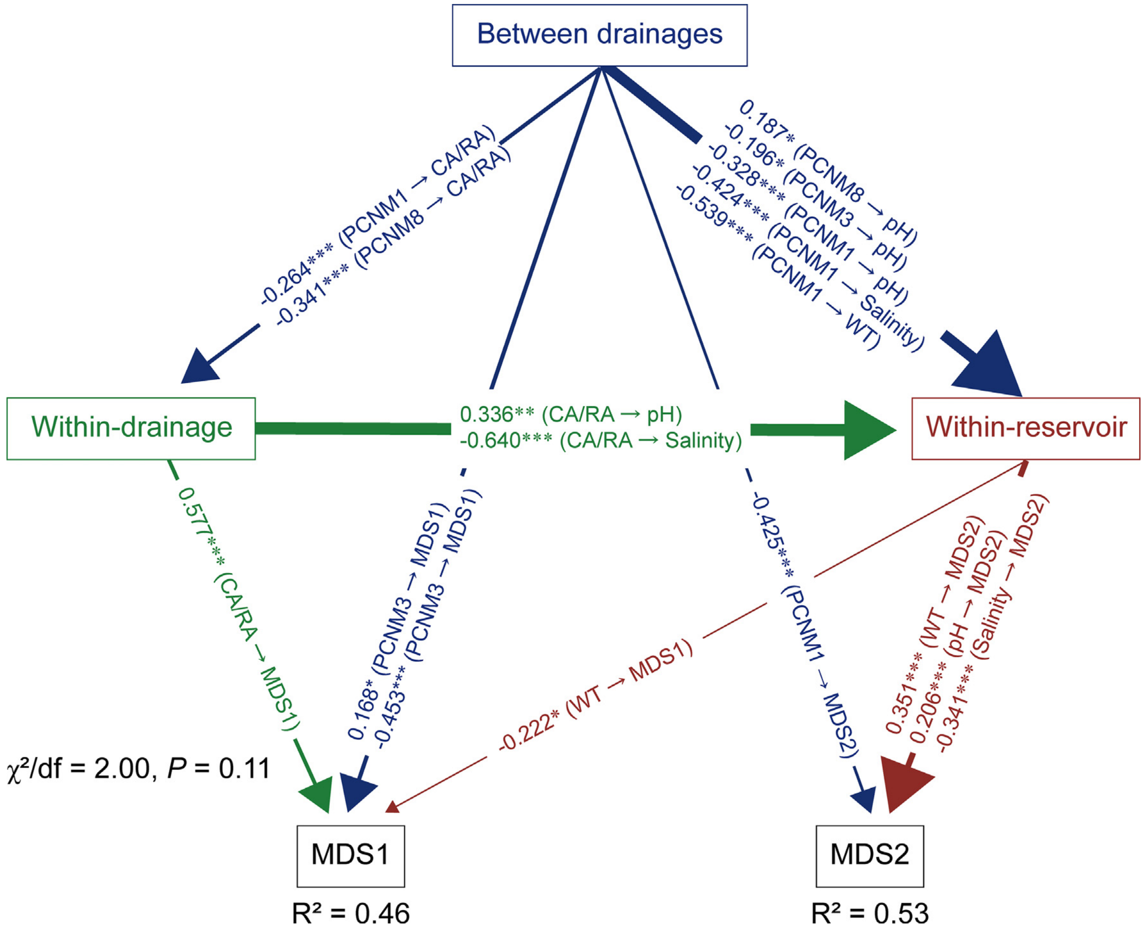

Fig. 5. Structural equation model (SEM) analysis showing the relationships between the spatial factors, environmental factors and the first two axes of zooplankton non-metric multidimensional scaling (NMDS) ordination based on 106 samples from 24 reservoirs in subtropical and tropical China. SEM co-variates are colored by corresponding scale (blue represents between drainages factors, green represents within drainage but between reservoirs factors, and brown represents within reservoir factors). Numbers near each arrow indicate partial correlation coefficients associated with each causal relationship, and arrow thickness is proportional to the sum of absolute values of the partial correlation value. The GFI (0.987), CFI (0.990), and $\chi^2/\mathrm{df} = 2.00$, $P = 0.11$) adjusted model indicated that the model was good fit to the original data.

composition to track environmental heterogeneity across large spatial scales effectively (Cottenie, 2005; Peres-Neto and Legendre, 2010).

But, at the same time, plankton in isolated drainage systems have only a limited ability to track environmental variation. In highly interconnected systems, changes in hydrological, physical and chemical factors at the local scale were emphasized in shaping the phytoplankton community, opposing the homogenizing effect of continuous dispersal (Vanormelingen et al., 2008; Qu et al., 2018; Isabwe et al., 2022). Therefore, the dispersal process could be attributed differently in isolated and connected drainage systems. In this study, the sampling reservoirs were located in subtropical and tropical China. Most rivers in this area are small with small watersheds, and they flow directly into the sea (Yang et al., 2012). The geographical isolation of plankton in different drainages was caused by the spatial barriers from the isolated reservoirs. Large reservoir area may have also resulted in habitat patch isolation and hindered the dispersal of many species. Habitat isolation can alter plankton community structure by environmental heterogeneity and food webs in the connected system (Yang et al., 2022). Thus, deep knowledge of the connectivity of drainage systems and the dispersal mechanisms will help to understand the spatial distribution of plankton communities at regional scale.

Species sorting consists of biotic interactions and environmental filtering. The species sorting process can filter suitable local species (Leibold et al., 2004). According to our VPA and SEM results, we can only provide evidence of the shaping mechanisms of environmental filtering on plankton community assembly. Ecological heterogeneity among species is another biotic community assembly mechanism (Bellier et al., 2014). Niche theory predicts that species-specific response to environmental gradients may cause ecological heterogeneity among species due to the species-specific growth rate (Bellier et al., 2014). Additionally, according to a recent study, bacteria made a great contribution to the nutrient cycle in reservoirs (Zhang et al., 2023). The abundance, composition, co-existence (Huang et al., 2022) and interactions (Zhang et al., 2022) of the bacterial community may affect the spatial distribution of phytoplankton and zooplankton communities. Thus, more studies about biotic interactions at a single trophic level and between trophic groups are needed to fill the knowledge gap in plankton community assembly mechanisms.

5. Conclusion

Our multi-scale data provide empirical support for the scale-dependence of spatial distribution of reservoir plankton communities. We demonstrated that the strength of the DDR patterns in plankton communities varied among three spatial scales in reservoirs in subtropical and tropical China. The slopes of DDRs were steepest within reservoirs, and they became shallower with increasing spatial scale in most cases. Our study provides strong evidence that both spatial and environmental variables contributed to the plankton DDRs, but the impact of spatial factors was overall greater. Phytoplankton and zooplankton communities were directly impacted by the environmental factors within-reservoir. The spatial factors and drainage characteristics affected plankton community distribution indirectly by influencing the local environmental factors. The heterogeneity of environmental factors among reservoirs is mainly caused by its spatial

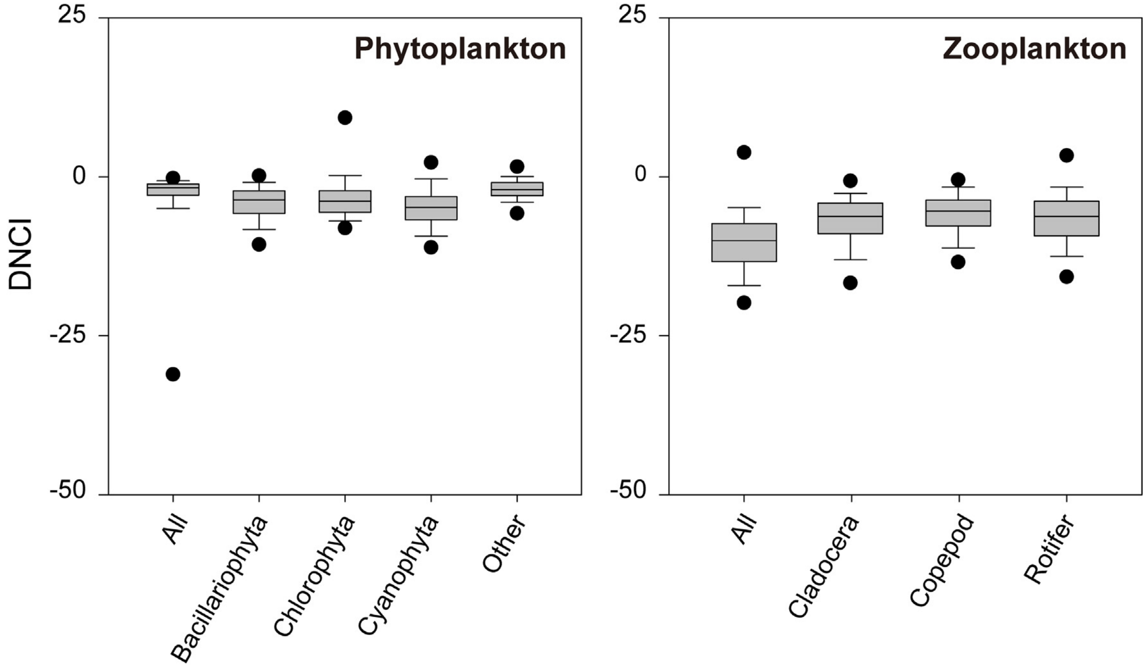

Fig. 6. Dispersal-niche continuum index (DNCI) values of plankton communities between 24 reservoirs from subtropical and tropical China. The DNCI values are computed for phytoplankton (All: the overall phytoplankton; Other: Chrysophyta, Cryptophyta, Euglenophyta, Pyrrophyta, and Xanthophyta) and zooplankton (All: the overall zooplankton) communities, respectively. Negative DNCI values indicate that dispersal is a more dominant assembly process than niche-based processes. Boxes and error bars indicate the 25th/75th and 5th/95th percentiles, respectively; middle line of the boxes is the median.

distribution (spatial factors) and the loading of drainage (catchment-level factors). Together, this study increases our understanding of spatial distribution in plankton communities and unveils the underlying mechanisms of plankton community assembly across a range of spatial scales.

CRediT authorship contribution statement

Lei Jin: Investigation, Methodology, Data Curation, Software and Writing – original draft.

Huihuang Chen: Investigation, Data Curation, Software and Writing – review & editing.

Yuanyuan Xue: Writing – review & editing.

Janne Soininen: Writing – review & editing.

Jun Yang: Conceptualization and Supervision, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157179.

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