Original Articles

Seasonal variation in the metacommunity structure of benthic macroinvertebrates in a large river-connected floodplain lake

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ABSTRACT

To improve our understanding on the temporal aspects of metacommunity structure, we focused on benthic macroinvertebrates collected seasonally (i.e., wet, drying, dry and rewetting seasons) in Dongting Lake, a large subtropical floodplain lake in China. We employed the elements of metacommunity structure (EMS) framework and variation partitioning to examine whether metacommunity structure and its underlying mechanisms vary among seasons with distinct biotic and abiotic features. We found gradual shifts in the main assembly mechanisms throughout the year, from apparent spatial structuring (potentially indicative of mass effects) in the wet season to more environmental filtering dynamics in the dry season. When the degree of connectivity was high in the wet season, the benthic metacommunity was characterized by nested structure associated with clumped species loss, and was shaped mainly by spatial processes. However, quasi-Clemensian structure was assigned to metacommunities in the transitional seasons with intermediate connectivity, during which environmental variables were more important than spatial factors in describing community structure. When the degree of connectivity was low in the dry season, the benthic metacommunity displayed Clementsian structure, which was configured solely by environmental variables. The rapid shifts in metacommunity dynamics between seasons mainly result from the considerable changes in the hydrological conditions of Dongting Lake, as the studied system varies from lacustrine to fluvial phases within a single year. Taken together, our results revealed that taking temporal aspects into account gives a better insight into metacommunity organization, especially when the studied systems embrace remarkable variability in hydrological regimes.

1. Introduction

Understanding patterns of species distributions and their underlying mechanisms is a core task in community ecology, macroecology and biogeography (Presley et al. 2009, Sutherland et al. 2013). In this respect, metacommunity ecology attempts to unravel how processes acting at local (e.g., abiotic filters and interspecific competition) and regional (e.g., dispersal) scales determine the coexistence and maintenance of species across sites scattered within a landscape (Leibold et al. 2004). To study metacommunity organization, several approaches have been proposed in recent decades (Vellend et al. 2014). The modelling approach focuses on comparing the relative influence of local and regional factors through differentiating the effects of environmental (proxy for species sorting) and spatial factors (proxy for dispersal

processes) by means of constrained ordination and associated variation partitioning (Cottenie 2005, Peres-Neto et al. 2006). However, this approach was questioned when being used to infer mechanisms, because of its inability to consider 1) all the potentially key environmental parameters, 2) interspecific interactions and 3) stochastic processes (e.g., Li et al. 2021c).

The pattern-based approach is an alternative to study metacommunity assembly by examining species distribution patterns with the Elements of Metacommunity Structure (EMS) framework. This framework compares an empirical metacommunity with multiple presupposed idealized typologies and assigns the best fit. Leibold and Mikkelson (2002) first proposed six fundamental typologies (for more details, see Table S1), including checkerboards (Diamond and Gilpin 1982), nested subsets (Patterson 1987), Clementsian gradients

(Clements 1916), Gleasonian gradients (Gleason 1926), evenly spaced gradients (Tilman 1982) and randomness (Simberloff 1978). Afterwards, Presley et al. (2010) subdivided nested subsets into three distinct scenarios of species loss (hyperdispersed-, random- and clumped- species loss), as well as defined six quasi-structures that are conceptually associated to gradient-driven structures and nested subsets. Owing to these recent methodological, conceptual and theoretical improvements, the EMS framework has been applied widely in various systems, including rivers (Erős et al. 2017), lakes (García-Girón et al., 2020), ponds (Richgels et al. 2013), forests (Marcilio-Silva et al. 2017), grasslands (Samu et al. 2018), and marine ecosystems (Yeh et al. 2015).

Integrating both approaches into the same study has been advocated for (Gascón et al. 2016). This is because, for example, the EMS analysis allows testing the possibility of random distribution compared with more structured patterns (Leibold and Mikkelson 2002), which partly compensate for the problems of variation partitioning (Henriques-Silva et al. 2013, Li et al. 2021c). However, despite the combination of both approaches has been recommended for a long time, relevant empirical studies are still inadequate and have emerged only recently (Yeh et al. 2015, Tonkin et al. 2017b). In addition, as most available studies have mainly been based on biotic and abiotic data obtained from a single period (i.e. 'snapshot' surveys), our knowledge regarding the temporal variability in these patterns and potential mechanisms is insufficient (Isabwe et al. 2018, Li et al. 2020). According to some recent studies, metacommunity structuring is typically complex and highly context dependent (Tonkin et al. 2016a, Sarremejane et al. 2017, Lansac-Tôha et al., 2021). This context dependency (e.g., seasonal variability in metacommunity patterns) would render the findings variable in time and thus hamper our attempts to generalize findings from one period to another (Csercsa et al. 2019, Sinclair et al. 2021). Consequently, snapshot surveys can only provide limited information on community assembly, and the investigation of metacommunities over time is thus becoming necessary and meaningful (Tonkin et al. 2018, Lindholm et al. 2020). This issue is of particular importance under the background of global change (Fahad et al., 2021a; Fahad et al., 2021b), since environmental conditions and patch connectivity are likely to change with climate variations and anthropogenic impacts at smaller scales (Heino et al. 2009, Sarremejane et al. 2017).

Floodplain ecosystems are among the most dynamic and heterogeneous systems, providing an ideal natural laboratory to examine temporal variation in metacommunity structures (Tonkin et al. 2016b, Diniz et al. 2021, Dong et al. 2021). In floodplains, local environmental conditions (e.g., water temperature, depth, current velocity and food resources) and patch connectivity vary continuously through time owing to seasonal shifts in the flow regime and local rainfall (Beche et al. 2006). These changes would in turn exert strong controls on the structures and the driving forces of aquatic metacommunities (Diniz et al. 2021, Lansac-Tôha et al., 2021). For example, flood pulses in the wet season may greatly increase the hydrologic connectivity among habitats, facilitating the dispersal of organisms as well as causing biotic and abiotic homogenization (Bozelli et al. 2015, Penha et al. 2017). At this juncture, spatial process (here, mass effects: strong source–sink dynamics allow species to exist in patches with suboptimal conditions) is likely to be predominant in structuring metacommunities (Fernandes et al. 2014). By contrast, during the dry phase when habitats are relatively isolated, local environments may become heterogeneous and species dispersal rates tend to be intermediate (Datry et al. 2016). This would enhance community dissimilarity and render environmental filtering as the prevailing force of community variation (Isabwe et al. 2018, Li et al. 2021b). However, empirical evidence on these temporal aspects of metacommunity dynamics in floodplain ecosystems is still deficient (Diniz et al. 2021), especially in the East Asian monsoon climate region.

Here, we integrated statistical modelling and the EMS framework to examine seasonal variation in species distribution patterns and the driving factors of metacommunities in a large floodplain shallow lake, Dongting Lake. Influenced by the East Asian monsoon, hydrological regimes (e.g., precipitation, discharge and water levels) vary considerably through time, which can be divided into four distinct water periods: wet, drying, dry and rewetting seasons (Fig. S1). During the wet period, it is a large river-connected lake characterized by stable discharge that maintains patch connectivity among habitats. However, during the dry season after the flood has receded, it is more like a river characterized by low water flow and thus reduced connectivity (Yu et al. 2018, Yang et al. 2020). We selected benthic macroinvertebrates as model organisms in this study, as they are diverse, sensitive to environmental changes, and play pivotal roles in food webs and ecosystem functioning (Li et al. 2021a). We asked the following questions and tested the associated hypotheses:

Q1: Do metacommunity structures of macroinvertebrates vary in different water periods (i.e., wet, drying, dry and rewetting)? We expected that the benthic metacommunity shows a nested pattern in the wet period, owing to the loss of some species by continual flooding, forming a set of nested subsets of successively larger assemblages (Fernandes et al. 2014). However, it is also possible that species distributions will display random patterns (Yeh et al. 2015), as flooding may promote random colonization and extinction (Diniz et al. 2021). In the transition and dry periods when this lake gradually transforms into fluvial facies and habitats are relatively isolated, benthic metacommunities may show gradient-related patterns (Clementsian or Gleasonian) (López-Delgado et al., 2019).

Q2: Do the relative importance of environmental filtering and spatial structuring change across seasons with distinct levels of connectivity? We hypothesized that spatial process will be more important in the wet period, in which high 'source-sink' dynamics (i.e., mass effects) at adjacent patches may obscure environmental control (Cai et al. 2019). As time passes, connectivity among patches will decrease, and environmental control may strengthen gradually at the expense of spatial structuring (Li et al. 2020). In other words, the effects of environmental filtering are expected to increase from i) the wet season to ii) the drying/rewetting season and then to iii) the dry season, while the opposite may be true for spatial structuring within a single floodplain lake.

2. Materials and methods

2.1. Study area

Located in the middle reaches of the Yangtze River, Dongting Lake (111°40′–113°10′ E, 28°30′–29°31′ N, Fig. 1) is the second largest freshwater lake in China (Yang et al. 2020). This lake is mainly fed by the Yangtze River and four tributary rivers (known as the 'Four Rivers': Li, Yuan, Zi and Xiang Rivers), creating a large river–lake compound ecosystem that support high array of freshwater biodiversity and endemic species (Meng et al. 2021). Affected by the subtropical monsoonal warm-humid climate, mean temperature is around 17°C, and mean precipitation reaches 1376 mm (Meng et al. 2018). Most of the precipitation is concentrated in the rewetting (April and May) and wet (June to September) periods, while only ca. 30% falls in the drying (October and November) and dry (December to March in the next year) seasons. Seasonal rainfall results in observable variability in hydrological conditions among seasons. For example, Dongting Lake covers a water surface area of approximately 2,670 km^2 in the wet season, but shrinks to ca. 710 km^2 in the dry season (Fig. S2). Its mean depth reaches about 18.7 m in the high-water periods, but reduces to ca. 6.4 m in low-water stages (Fig. S1) (Geng et al. 2021). This lake plays an important role in flood control, drinking and irrigating water supply, as well as biodiversity conservation. Much is known about the lake's climatic features, hydrological conditions, water quality and flagship species, including the Yangtze finless porpoise and the Chinese sturgeon, which have been included in the national long-term monitoring programs (Guo et al. 2020, Yang et al. 2020, Geng et al. 2021). However, little is known about the temporal variability in metacommunity structures of small but
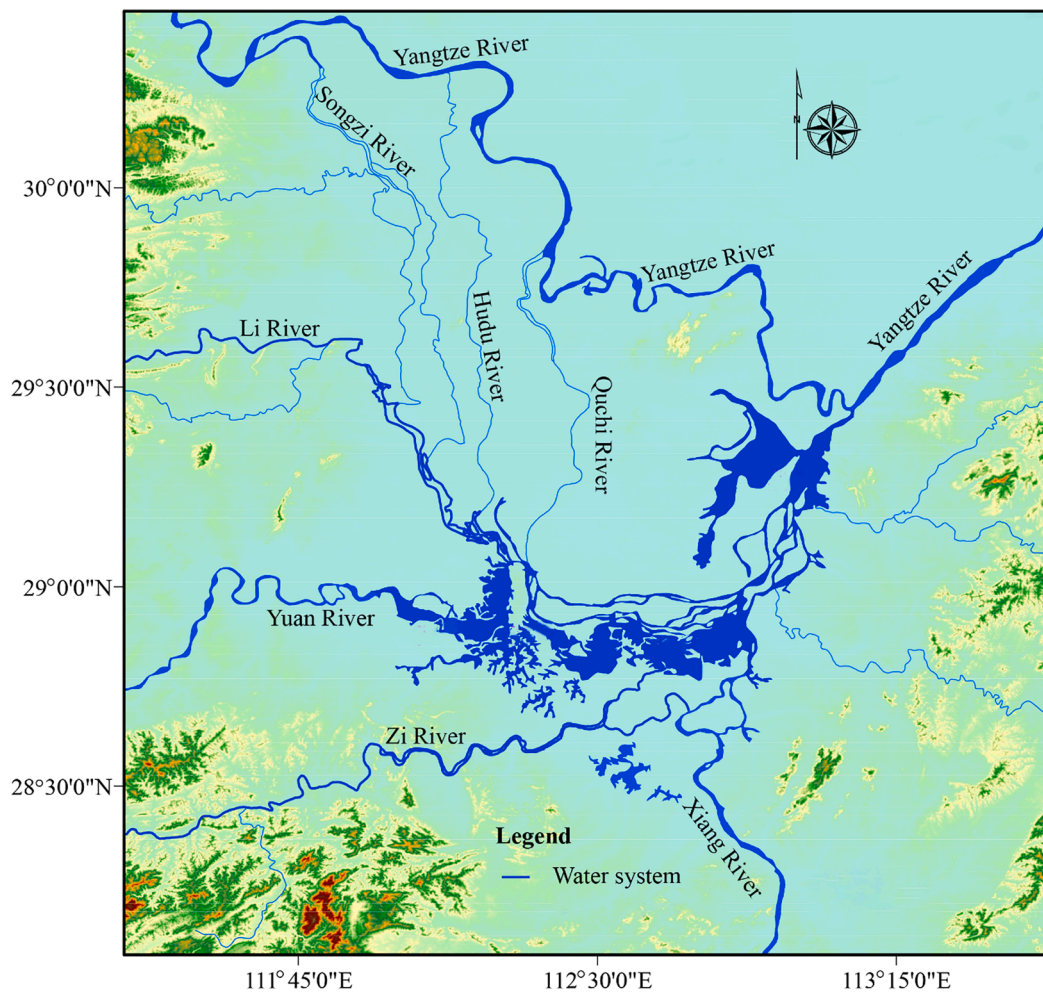
Fig. 1. Sampling sites of benthic macroinvertebrates in Dongting Lake.

important lake-dwelling organisms (e.g., invertebrates), let alone the various underlying mechanisms of biotic variation.

2.2. Macroinvertebrate sampling

Benthic macroinvertebrates were sampled from the same 42 sites in Dongting Lake during the wet, drying, dry and rewetting seasons in 2018. Three sediment samples were obtained with a Petersen grab (0.065 m^2) at each site, and then were subsequently sieved with a copper sieve (500 μm in mesh size) in the field (Meng et al. 2018). Samples were provisionally stored in a deepfreeze, and were taken to the field station. In the station, benthic animals were hand-picked from the sediments, and were then preserved in 10% formalin. Specimens were identified to genus or species level with a dissecting microscope according to the available references (Liu et al. 1979, Morse et al. 1994, Dong et al. 2005, Oscoz et al. 2011, Wiggins 2018) as well as online resources (National Animal Collection Resource Center, http://museum.ioz.ac.cn/index. html).

2.3. Environmental variables

Prior to macroinvertebrate sampling, we measured local environmental parameters on each sampling occasion. Water transparency was determined with a Secchi dish, and depth was measured using a TDSS-100 ultrasonic depthometer. Water temperature, pH, dissolved oxygen, total dissolved solids and conductivity were recorded using a Multiparameter water quality analyzer (YSI EXO2). Current velocity was measured at five random locations at each site with an LJD-10 flowmeter. Sediments were classified into three categories (i.e., silt, hard clay and sand) through visual observation, and were coded into numbers using dummy variables. Afterwards, water samples were collected with an acrylic sampler, and were kept in the refrigerator before taking to the laboratory for measurements. In the laboratory, six water chemical parameters (i.e., total phosphorus, orthophosphate, total nitrogen, ammonium nitrogen, nitrate nitrogen and chemical oxygen demand) were measured based on relevant standards for water chemistry measurement in China (Huang et al. 1999).

2.4. Spatial factors

Spatial factors was employed as proxies for dispersal processes (Borcard et al. 2004). To create spatial factors, Moran's Eigenvector Maps (MEM) was applied based on between-sites Euclidean distances calculated from geographic coordinates (x and y) (Blanchet et al. 2008). MEMs (i.e., spatial eigenvalues) can model the spatial structure of biological assemblages at multiple scales, and can be used to represent dispersal processes, biogeographic effects, as well as environmental autocorrelation (Dray et al. 2012). We retained the MEM vectors associated with positive eigenvalues and significant Moran's I as they represent a positive spatial autocorrelation. Higher MEMs eigenvalues indicate broad-scale relationships among sites, while low MEMs imply fine-scale spatial patterns in species distributions. MEM was conducted using the PCNM package in R (Legendre et al. 2012).

3. Data analysis

3.1. Environmental characteristics

One-way, repeated-measures analysis of variance (ANOVA) was first employed to examine the differences of environmental factors (log-transformed when data violated normality) among the seasons. The repeated-measures analysis was chosen because the same sites were sampled on four subsequent occasions, resulting in temporally non-independent data. Increasing hydrological connectivity typically decreases between-site environmental heterogeneity, which may preclude examining the effects of connectivity on community assembly mechanisms (i.e., environmental vs. spatial factors) in different time periods. Therefore, permutational analysis of multivariate dispersions (PERM-DISP) was employed to compare environmental heterogeneity among seasons (Anderson and Walsh 2013). This analysis examines the differences of the average distance of sampling sites to group centroid in a multivariate space. Therefore, the larger the average distance from the centroid, the grater the environmental heterogeneity of the study area. PERMDISP was conducted based on Euclidean distances of normalized environmental parameters (except for pH).

3.2. Species composition

Canonical analysis of principal coordinates (CAP) was applied to distinguish the average differences in species composition among the four seasons. This analysis is a variant of principal coordinates analysis (PCoA), aiming to find axes that best discriminate among a priori groups in a multivariate cloud of points. This analysis can be conducted based on any type of resemblance matrix. Afterwards, one-way analysis of similarities (ANOSIM) with 999 permutations was employed to test if the seasonal differences in species composition were significant. CAP and ANOSIM were run based on Bray–Curtis similarity matrices for log-transformed macroinvertebrate abundance data. Then, similarity percentage analysis (SIMPER) analysis was utilized to recognize the species that contributed most to similarity of species composition within each season (Clarke 1993). ANOVAs were conducted in SPSS statistical programs (22.0), while PERMDISP, CAP, ANOSIM and SIMPER were run with PERMANOVA + for PRIMER (Anderson et al. 2008).

3.3. Idealized metacommunity structures

The Elements of metacommunity structure (EMS) framework (Leibold and Mikkelson 2002, Presley et al. 2010) was applied to identify the idealized structures of benthic metacommunities in each season. By analyzing three elements (i.e., coherence, species turnover and boundary clumping) of species distributions, the EMS approach attempts to seek out the idealized structure or quasi-structure that best associated to an empirical metacommunity (Fig. 2). These elements and their respective significance were evaluated hierarchically with null model analysis based on permutation tests. Before assessing the three elements, taxa that occurred at only one site were excluded (to avoid the possibility of bias in the EMS results), and then incidence matrix (presence–absence data) was ordinated through reciprocal averaging (CA).

The EMS analysis follows a three-step process. Firstly, we assessed coherence (denoting whether species respond to the same latent gradient) by calculating the number of embedded absences within species ranges and comparing the observed value to a null distribution with a z-score test. Negative coherence (a metacommunity have more embedded absences than expected by chance) is indicative of a checkerboard structure, whereas non-significant coherence means that the distributions of species are random (Fig. 2). Positive coherence (a metacommunity has fewer embedded absences than expected by chance) suggests that species distributions are responding similarly to an environmental gradient.

Afterwards, species turnover (depicting how species replacing each other among sites along latent gradient) was examined only if the empirical metacommunity showed positive coherence. Turnover was evaluated by counting the number of times a species was replaced by another species between two sites and then comparing the observed value to a null distribution using a z-score test. If turnover is significantly negative (fewer replacements than expected), a metacommunity exhibits a nested pattern (i.e., hyper-dispersed species loss, random species loss, and clumped species loss). In contrast, a metacommunity may be classified as gradient-like pattern (i.e., evenly spaced, Gleasonian or Clementsian gradients) if turnover is significantly positive (more replacements than expected). If turnover is not significant, an empirical metacommunity would be categorized as one of the six quasi-structures (Fig. 2).

Finally, boundary clumping (describing whether species ranges have similar boundaries) was assessed with Morisita's index (MI) of dispersion associated using a χ2 test that compares the empirical distribution of range boundaries to an expected uniform distribution. When turnover was significantly positive, MI values significantly higher than 1, significantly less than 1 and not significantly different from 1 indicate Clementsian, evenly spaced and Gleasonian gradients, respectively. When turnover is significantly negative, the aforementioned three cases of MI values would refer to clumped, hyper-dispersed and random species losses in sequence. Correspondingly, when turnover is not significant, series of quasi-structures are possible following the logic of the
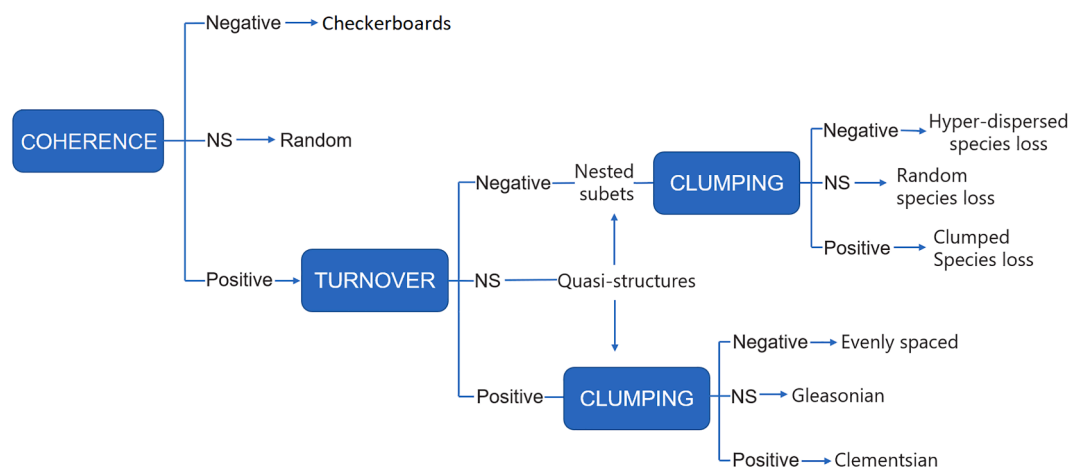

Fig. 2. A chart describing the theoretical framework of the Elements of metacommunity structure (EMS) analysis, showing how eight idealized metacommunity typologies and six Quasi-structures are differentiated. Figure modified from Presley et al. (2010). NS: non-significant.

previous sentences (Fig. 2).

The EMS analysis was performed with the "Metacommunity" function in the R package metacom (Dallas, 2018). The significance of coherence and range turnover was tested using the fixed-proportional null model (999 permutations), in which species richness of each site was maintained and species ranges are filled based on their marginal probabilities. The idealized patterns were assigned according to prior relevant references (Leibold and Mikkelson 2002, Presley et al. 2009, Presley et al. 2010).

3.4. Driving forces

Distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999) based on Bray–Curtis resemblance matrix was employed to determine the key environmental and/or spatial variables relating to benthic assemblages. Before variables selection, the statistical significance of the full model (i.e., dbRDA models considering all the environmental or spatial factors) was tested with the "anova.cca" function in vegan package (Oksanen et al. 2019). When the full model was significant, a forward selection procedure using the function 'ordiR2step' in vegan was applied to separately select the environmental and spatial factors that significantly associated with macroinvertebrate community variation. To examine the relative importance of different driving mechanisms, variation partitioning analysis (VPA) was conducted with the function "varpart" in the R package vegan (Oksanen et al. 2019). Total variation in metacommunity structure was partitioned into pure environmental (E | S), pure spatial (S | E), shared (E ∩ S) and unexplained (U) fractions. These fractions were showed based on adjusted R^2 values, because they are unbiased estimates of explained variation (Peres-Neto et al. 2006). Finally, we tested the significance of the pure fractions (i.e., E | S and S | E) with the "anova.cca" function.

4. Results

4.1. Environmental characteristics and species composition

More than half of the 14 analyzed environmental parameters differed significantly ($p < 0.05$) among the four water periods. Specifically, physical properties (e.g., WT, EC, DO, MD, LT, TDS and CV) of this lake displayed great seasonal fluctuations, while chemical characteristics (except for NH_4-N and COD_{Mn}) were relatively stable over time (Table 1). PERMDISP analysis revealed that local environmental conditions in the dry season were relatively more heterogeneous than those in the other three seasons (Fig. 3).

Overall, 108 macroinvertebrate taxa were identified, which belong to seven classes, 18 orders and 43 families. A greater number of taxa (65) and individuals (6132) was detected in the wet season, when compared
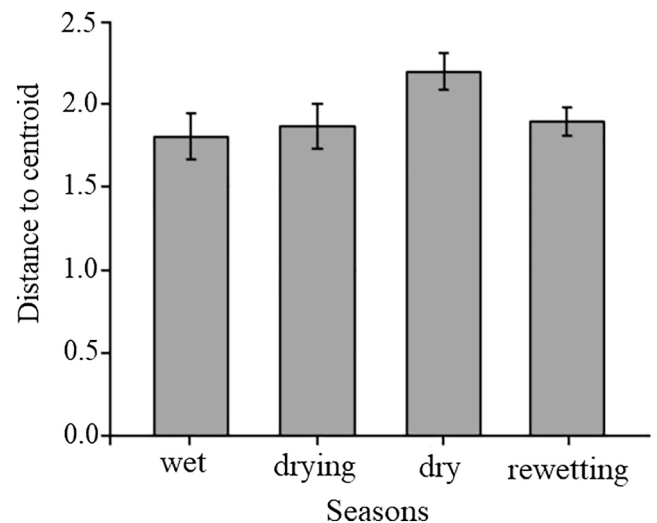

Fig. 3. PERMDISP analyses based on Euclidean distance of environmental data from different seasons, showing the mean distance to group centroid and standard error (SE) in each season.

to those in the drying (36 taxa and 4105 individuals), dry (34 and 4861) and rewetting (40 and 5257) periods (Table S2). According to the CAP analysis, species composition showed considerable variability among seasons (Fig. 4), and this finding was further reinforced by the ANOSIM analysis (R = 0.189, $p < 0.001$). SIMPER analyses showed that during the wet season, *Bellamya aeruginosa*, *Gammarus* sp., *Rivularia auriculata*, *Corbicula fluminea* and *Dicrotendipes* sp. were numerically dominant and jointly accounted for up to 79.22% of the within-group similarity. The drying season was dominated by *Corbicula fluminea*, *Gammarus* sp., *Branchiura sowerbyi*, *Limnoperna lacustris* and *Limnodrilus hoffmeisteri* which accounted for up to 85.77% with-group similarity. The dry season was dominated by *Gammarus* sp., *Corbicula fluminea*, *Cryptochironomus* sp., *Stictochironomus* sp. and *Orthocladius* sp., which accumulatively explained 71.58% within-group similarity. Finally, *Corbicula fluminea*, *Limnodrilus hoffmeisteri*, *Bezzia* sp., *Limnoperna lacustris* and *Cryptochironomus digitatus* numerically dominated in the rewetting season, explaining up to 86.24% within-group similarity (Table S3).

4.2. Seasonal variation in idealized metacommunity structures

The first step of the EMS showed that coherence was significantly positive (z-score < 0) in each season, indicating that species in general responded to the same environmental gradient. However, relatively different patterns were observed through time by evaluating range

Table 1
Results of One-way, repeated-measures analysis of variance (ANOVA), also showing the mean value (Mean) and standard deviation (SD) of environmental variables at the four sampling periods in Dongting Lake. Bold values indicate statistically significance at $p < 0.05$.

| Environmental variables	Abbreviation	wet Mean	SD	drying Mean	SD	dry Mean	SD	rewetting Mean	SD	F	p
Water temperature (℃)	WT	30.44	1.78	20.39	0.80	9.34	0.58	17.70	1.33	298.59	**< 0.001**
Conductivity (µs/cm)	EC	293.61	40.61	272.28	286.53	169.48	47.45	259.97	64.14	5.86	**0.004**
Dissolved oxygen (mg/L)	DO	4.79	1.23	7.56	0.87	10.09	0.79	9.37	1.70	273.38	**< 0.001**
pH	pH	8.27	0.30	8.15	0.28	8.33	0.14	8.25	0.45	0.95	0.388
Mean depth (m)	MD	9.28	7.99	7.42	9.02	4.07	2.57	4.91	2.52	5.14	**0.007**
Lake transparency (m)	LT	0.62	0.49	0.45	0.17	0.39	0.11	0.41	0.24	5.68	**0.004**
Total dissolved solids	TDS	181.30	19.49	161.60	31.52	158.90	42.20	163.20	28.04	5.51	**0.005**
Current velocity (m/s)	CV	0.34	0.11	0.31	0.08	0.29	0.06	0.30	0.13	3.62	**0.030**
Total nitrogen (mg/L)	TN	2.08	0.84	1.74	1.20	2.06	0.93	2.12	0.58	1.4	0.251
Total phosphorus (mg/L)	TP	0.18	0.25	0.15	0.36	0.08	0.05	0.16	0.10	1.48	0.231
Nitrate (mg/L)	NO_3-N	1.01	0.66	0.99	0.35	1.21	0.44	1.49	0.58	2.27	0.108
Ammonium nitrogen (mg/L)	NH_4-N	0.67	0.69	0.22	0.44	0.61	0.45	0.57	0.36	19.25	**< 0.001**
Orthophosphate (mg/L)	PO_4-P	0.07	0.11	0.06	0.03	0.05	0.02	0.13	0.07	1.43	0.242
Chemical oxygen demand (mg/L)	COD_{Mn}	3.14	1.23	2.56	0.88	2.81	1.24	2.76	1.05	4.11	**0.019**
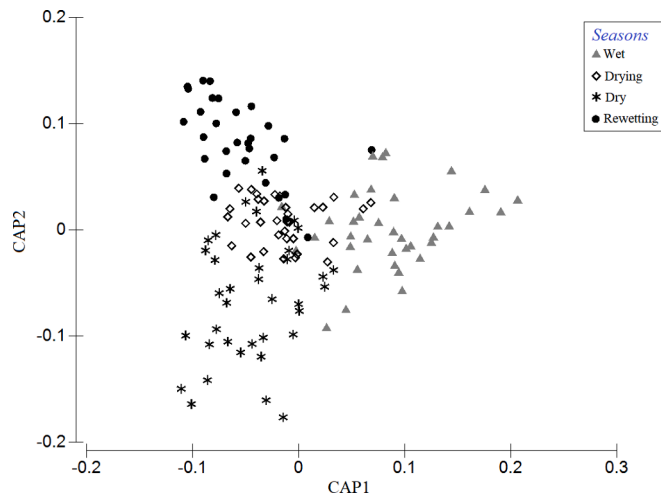
Fig. 4. Canonical analysis of principal coordinates (CAP) ordination plot based on Bray-Curtis similarity matrices calculated from abundance data of macro-invertebrate assemblages.

turnover (Table 2). Turnover was significantly negative for the macro-invertebrate metacommunity during the wet season (indicative of nested subsets), but was significantly positive in the dry season (indicative of gradient-related structures) (Table 2; Fig. 2). For the meta-communities in both rewetting and drying seasons, turnover was positive but statistically non-significant (indicative of quasi- gradient-related structures). Lastly, the metacommunity in each season showed significantly positive boundary clumping (Morisita's index > 1), implying that changes in community structure were mainly result from taxa groups being different among sites. Thus, the idealized typologies that best fit the observed metacommunity structures in the four seasons were: clumped species loss (wet season), quasi-Clementsian gradients (drying and rewetting seasons) and Clementsian gradients (dry season) (Table 2).

4.3. Seasonal variation in driving forces

The total explained variation in metacommunity structures of lake macroinvertebrates ranged from 16.0% to 22.1% (Table 3). Both environmental and spatial factors played important roles in regulating benthic assemblages, although their number, identity and relative

Table 2
Results of analyses of coherence, species turnover and boundary clumping for lake macroinvertebrate metacommunities in the wet, normal, dry and rewetting seasons. The best-fitting metacommunity structures are also determined.

	wet	drying	dry	rewetting
Coherence				
Observed absences	1123	428	680	400
Expected absences	1442	795	950	618
z-score	−4.73[***]	−8.42[***]	−5.50[***]	−6.97[***]
Turnover				
Observed replacements	25,508	21,475	43,140	19,616
Expected replacements	38,547	20,996	31,782	15,913
z-score	−3.02[**]	0.19	2.13[**]	1.28
Clumping				
Morisita's index	1.66[***]	1.39[**]	1.37[**]	2.66[***]
Best-fitting structures	Clumped species loss	quasi-Clementsian	Clementsian	quasi-Clementsian

**p < 0.01
***p < 0.001

Table 3
Results of distanced-based redundancy analyses (dbRDA) and variation partitioning, showing the relative influence of significant environmental and spatial variables on metacommunity structure of macroinvertebrate in each season. Values for each explained fraction are adjusted R^2. Fractions are variations explained by [E | S] pure environmental, [S | E] pure spatial and [E ∩ S] shared effects, and [U] unexplained variations. The meaning of abbreviations of environmental variables (e.g., LT and TN) can be found in Table 1.

Fractions	df	Adj. R^2	p	Key variables retained in the model
wet				
E	5	0.093	0.001	LT, TN, WT, Silt, Hard clay
S	6	0.136	0.001	MEM1, MEM2, MEM3, MEM6, MEM7, MEM19
E + S	11	0.174	0.001	All variables above
E|S	5	0.038	0.002	
E ∩ S		0.055		
S|E	6	0.081	0.001	
Residual		0.826		
drying				
E	5	0.155	0.001	COD$_{Mn}$, Silt, TDS, NH$_4$-N, pH
S	3	0.072	0.001	MEM17, MEM3, MEM4
E + S	8	0.221	0.001	All variables above
E|S	5	0.149	0.001	
E ∩ S		0.006		
S|E	3	0.066	0.002	
Residual		0.779		
dry				
E	4	0.171	0.001	TP, LT, WT, TN
Residual		0.829		
rewetting				
E	3	0.127	0.001	TP, EC, MD
S	2	0.070	0.001	MEM1, MEM8
E + S	5	0.160	0.001	All variables above
E|S	3	0.090	0.001	
E ∩ S		0.036		
S|E	2	0.033	0.003	
Residual		0.840		

importance varied considerably through time. In the wet season, as expected, the pure effect of spatial factors (S | E) was obviously more influential than that of environmental variables (E | S) (8.1% vs. 3.8%). In contrast, during the drying and rewetting seasons, variations were better explained by environmental variables than by spatial factors (14.9% vs. 6.6% in the drying season; 9.0% vs. 3.3% in the rewetting season). Only environmental variables (17.1% of total variation explained) were found to be significant determinants of community structure in the dry season (Table 3). The shared effects between environmental and spatial factors (E ∩ S) also explained certain percentage of community variation but were much lower than those of pure effects. Moreover, there was still a large percentage of variation (ca. 80%) unexplained by the spatial and environmental factors in combination (Table 3).

5. Discussion

Many previous studies on metacommunities have focused on snapshot surveys. These studies, however, overlook the temporal variability in metacommunity dynamics, which is particularly apparent for organisms in heterogeneous floodplain ecosystems (Bozelli et al. 2015, Dong et al. 2021). In the present study, we focused on benthic macroinvertebrates inhabiting a large floodplain lake under the influence of a subtropical monsoon climate, with considerable hydrologic variability through the year. By integrating two complementary approaches (i.e., the EMS framework and variation partitioning), we investigated the idealized metacommunity structures and inferred underlying mechanisms of community assembly in four seasons characterized by different environmental features and hydrological connectivity. We found that macroinvertebrate metacommunities showed distinct best-fit patterns throughout the four sampling periods. These idealized patterns included nested, quasi-Clementsian and Clementsian structures, which were

commonly found in previous metacommunity studies in lakes (García-Girón et al., 2020, Diniz et al. 2021, Lech and Willig 2021) and rivers (Tonkin et al. 2016c, Vieira et al. 2020). The relative contribution of ecological factors (environmental and spatial variables) regulating these patterns also differed among seasons. These findings support the idea that temporally repeated surveys can provide a fuller picture of meta-community organization than snapshot studies, by which one can make more robust inferences of ecological phenomena (Fernandes et al. 2014, Lansac-Tôha et al., 2021).

As expected, the benthic metacommunity in the wet season showed a nested pattern with negative range turnover and clumped species loss. This finding was reasonable because some sites may lose a cluster of taxa that cannot withstand the continual flooding and the drastic changes in abiotic conditions. These taxa may find refugia in some parts of the lake to wait for the chances to increase in abundance again, thus occupying only limited numbers of sites. At the same time, other taxa that favored the new conditions would multiply rapidly and broaden their distributions facilitated by 'source–sink' dynamics (sensu Pulliam 1988). It is also possible that benthic macroinvertebrates exhibited variable dispersal potential, driving their variable distributions (Meng et al. 2020, Dong et al. 2021). For instance, flood-related drift allowed some small and flexible taxa (e.g., *Gammarus* sp.) to occupy most, if not all, sites, whereas some larger taxa (e.g., *Lamprotula caveata*) only appeared sporadically in this lake. As a consequence, the ranges of taxa with confined distributions along the environmental gradient were contained in the ranges of taxa that were widely distributed, forming a nested pattern (Presley et al. 2010).

The results of variation partitioning also potentially supported the existence of 'source–sink' (or mass effects) dynamics in the wet season, as spatial factors prevailed over environmental variables in shaping metacommunity structure. It has been suggested that both dispersal limitation and mass effects can induce spatial structuring seen in the biological data (Heino et al. 2015, Chaparro et al. 2018). However, we conjectured that mass effects were more likely to play the leading role here, because extensive dispersal is more likely to occur in water bodies with high connectivity (Tolonen et al. 2017), such as lakes (Cai et al. 2019), mainstem rivers (Brown and Swan 2010) and marine coastal systems (Yeh et al. 2015). In the mass effects paradigm, high rates of dispersal and subsequent continuous colonization allow species to occur in non-suitable patches irrespective of local environmental conditions, thus obstructing the performance of environmental control (Leibold et al. 2004, Diniz et al. 2021). Actually, in the wet period, Dongting Lake itself acted as a large 'sink', which constantly recruited species from the nearby 'source' rivers (e.g., the Yangtze River and the 'Four Rivers') owing to the increased river–lake connectivity. This provides an explanation for why we collected more taxa and individuals in the wet season compared to the other sampling periods.

When Dongting Lake transformed into fluvial conditions in the dry season, Clementsian structure characterized by high coherence and turnover as well as positive boundary clumping was identified for benthic macroinvertebrates. Clementsian structure indicates that the metacommunity is composed of discrete species that exhibit similar responses to environmental gradients and replace in groups across space (Clements 1916, Leibold and Mikkelson 2002). This typology is often correlated with environmental filtering in community assembly (López-Delgado et al., 2019, Diniz et al. 2021). Indeed, this inference was reinforced by variation partitioning results, as the benthic meta-community appeared to be more determined by local environmental filters than spatial processes. During the dry season following flood recedence, some originally well-connected habitats lost connectivity to other locations and became relatively isolated (Dong et al. 2021). As a result, reduced dispersal rates hindered the rapid patch colonization of organisms (reflecting mass effects), generating discrete community types typified by high species turnover. This amount of dispersal may also facilitate species to track environmental gradients among patches. Therefore, species were selected by environmental variables to occur

only at environmentally suitable sites, suggesting association with the species sorting paradigm (Leibold et al. 2004). Clementsian structure may also derive from competitive interactions, if pairs of competing species (i.e., 'forbidden combinations') do not occur independently of each other, rather forming 'clusters of forbidden combinations' (Gilpin and Diamond 1982, Henriques-Silva et al. 2013, Fernandes et al. 2014). This is possible, because flood recession may reduce the availability of aquatic habitats and food resources, which may increase interspecific competition (Rodríguez and Lewis, 1997). However, to test the possibility of competition, further studies are needed and may benefit from the use of phylogenetic or trait-based approaches as proxies of competitive interactions (Ge et al. 2021).

Quasi-Clementsian structure was assigned to benthic meta-communities during the transitional (i.e., drying and rewetting) periods when connectivity was intermediate. This typology usually occurs when species range turnover is not distinguishable from randomness, indicating weaker structuring mechanisms than those in regular Clementsian structure (Tonkin et al. 2017b). It can be inferred that the relative role of environmental filtering at these periods was not as strong as during the dry season. This conjecture was supported by the results of variation partitioning, in which transitional metacommunities were determined by both environmental and spatial effects. However, it seemed that dispersal rates of organisms at this occasion were not high enough to generate strong spatial signals that surpassed local environmental control. Therefore, metacommunity organization was still better explained by environmental filters than by spatial effects in the transitional seasons. Our results thus suggested that environmental filtering may explain most of the variation in community structure most of the time throughout a year. This finding corroborated the prior idea that species sorting may be the most prevalent metacommunity paradigm for assemblages in aquatic ecosystems (Cottenie 2005, Soininen 2014, López-Delgado et al. 2019).

In a review on metacommunity organization in aquatic systems, Heino et al. (2015) proposed the optimal spatial scales at which multiple ecological mechanisms would be expected to dominate. They conjectured that environmental filtering would be dominant at intermediate spatial extents, while spatial structuring may be more influential at fine (mass effects) and broad (dispersal limitation) scales. However, they did not mention how these mechanisms vary through time; instead, they emphasized the importance of exploring temporal aspects of meta-community dynamics in further studies. Here, we illustrated this temporal variability of community assembly in a floodplain lake with a schematic diagram, in which the relative role of environmental and spatial effects fluctuated depending on the sampling periods (Fig. 5). In this diagram, spatial structuring dominated in the wet period with high connectivity. As time progressed, the relative importance of the driving forces switched, with environmental filtering strengthening as spatial structuring dissipated. The effect of environmental filtering peaked during the dry season, a period when spatial structuring barely worked. Afterwards, environmental filtering decreased in importance, and spatial structuring gradually intensified and attained the peak again. However, this hypothesis was deduced based solely on samples collected at four different time periods within a single year from one floodplain lake. We emphasize the need for further studies to consider different biological groups, different habitat types, and different underlying hydro-climatic forcing, as well as increase sampling frequency to test the generalization of this hypothesis.

According to the theory of temporal niche dynamics (Chesson 2000), temporal fluctuations in hydrological and environmental conditions allows different species to utilize resources at different time periods, buffering species against extinction as well as promoting species coexistence and increasing diversity (Tan et al. 2013, Tonkin et al. 2017a). This may help explain why some temporally heterogeneous systems, such as Dongting Lake, hold disproportionately high biodiversity. However, under the impacts of climate change and anthropogenic activities, especially after the construction of the Gezhou Dam and Three
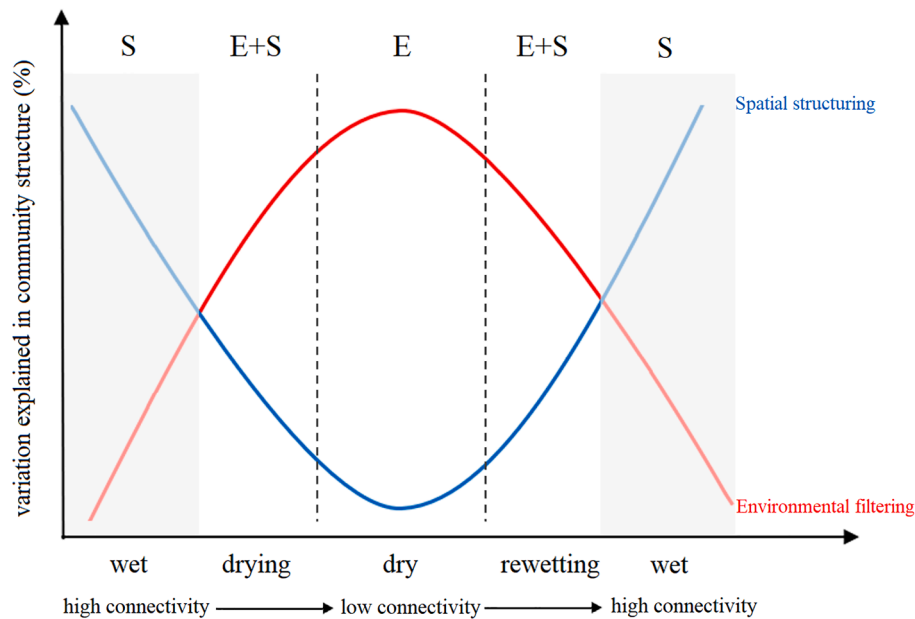
Fig. 5. Schematic diagram showing metacommunity organization of macroinvertebrates in the river-connected lakes in floodplain ecosystems. Figure adapted from Heino et al. (2015). Environmental filtering [E] and spatial structuring [S] mean variation in community structure explained purely by pure environmental and spatial factors.

Gorges Dam in the mainstem Yangtze River in recent years, annual water discharge in this lake is decreasing (Yu et al. 2018, Peng et al. 2021). As a consequence, we see a tendency of less flooding in time of the flood season and more drying during the dry season (Yang et al. 2020). Altered seasonal fluctuations in abiotic conditions will continue to influence metacommunity dynamics and species diversity in the lake. During some arid periods, reduced water level will cause habitat loss, alter community structure and consequently, ecosystem functions including the maintenance of biodiversity. For example, large bivalves, that can help purify water quality (via filter-feeding behavior) and provide high-grade protein for humans, are known as ecologically and economically important species. However, large bivalves are also very sensitive to the drastic changes in environmental and hydrological conditions, owing to their weak environmental tolerance and weak dispersal capacity to escape drought. If drought continues, these important species may be gradually dying out for lack of stable living conditions. Therefore, we urge the establishment of a long-term monitoring program on the ecological impacts of dams at the metacommunity level and to mitigate any adverse effects on environmental conditions and ecological communities when necessary. For example, evaluating the minimum water requirement of organisms during the dry season and then retain water to keep a certain degree of connectivity and water volume, may be important to sustain biodiversity and ecosystem function under the influence of cascade dams and environmental change. However, to solve this problem radically, we still need to integrate varieties of measures involving those from political, technical, financial and social realms.

6. Conclusions and recommendations

In the present study, we focused on examining seasonal variation in the metacommunity structures and driving forces of macroinvertebrate assemblages in a large floodplain lake. Generally, we found that metacommunities showed different idealized structures among seasons. In the wet season, the benthic metacommunity was characterized by nested structure associated with clumped species loss. However, quasi-Clemensian and Clemensian structures were assigned to metacommunities in the transitional and dry seasons, respectively. The driving forces of community variation also changed through time.

Spatial structuring was more influential for communities in the wet season, while environmental filtering was more important during the transitional and dry seasons. These results gives a better insight into metacommunity organization at temporal scales. This study also have certain implications for the applied field, such as biodiversity conservation. For example, as metacommunity structures changed with hydrological connectivity and environmental conditions, future climate change and water retaining dams would inevitably impact metacommunity dynamics and biodiversity. Thus, taking effective measures from multi-field to mitigate these adverse effects is urgently needed. Finally, for ecological indicators to evaluate the health of this lake, we recommend using the identity, density and richness of large bivalves (e. g., *Lamprotula caveata*, *Lamprotula leai* and *Schistodesmus lampreyanus*), as they play a vital role in lake ecosystems and are sensitive to environmental change.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ecolind.2022.108662.

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