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Differences in diversity and community assembly processes between planktonic and benthic diatoms in the upper reach of the Jinsha River，China

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Abstract: Comparing the spatio-temporal patterns between planktonic and benthic diatoms is helpful to understand biodiversity patterns and drivers in rivers. However, such studies are still rare especially in mountain regions. We used a dataset collected in the upper reach of the Jinsha River in different seasons to explore biodiversity and assembly processes of planktonic and benthic diatom assemblages. We found that planktonic and benthic diatoms presented different seasonal variation in species richness and community composition. We also found evidence that planktonic and benthic diatoms were coupled especially in the summer. Planktonic diatom assemblages were mainly affected by spatial processes (mainly directional spatial processes) in both seasons. The effects of environmental processes were significant in the autumn, but were almost negligible in the summer. By comparison, benthic diatom assemblages were more affected by environmental factors than spatial processes. Our results suggested that mass effect and species sorting paradigms explained the assembly processes of planktonic and benthic diatom assemblages, respectively, but the explanatory powers of these two paradigms varied seasonally. To effectively monitor and assess river environmental conditions, we recommend using benthic algae as a biotic indicator group as they seem to better reflect environmental conditions in rivers.

Keywords: metacommunity; species sorting; mass effect; directional spatial processes; seasonal dynamics

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Introduction

Lotic algae can be divided into planktonic and benthic algae. Planktonic algae mainly live in water column and usually move passively to downstream with water flow while benthic algae attach to various substrates immersed in water and do not move easily. Benthic algae are dominant in headwaters and low-order streams or shallow rivers, whereas planktonic algae are more abundant in large rivers (Kireta et al., 2012). Although these two algal groups differ in habitat preference and dispersal ability, planktonic and benthic algae can coexist in rivers where they are coupled and compete with each other in a dynamic equilibrium state (Jäger & Diehl, 2014; Wang et al., 2019). On one hand, planktonic and benthic assemblages are generally closely coupled through sedimentation and resuspension (Werner & Köhler, 2005; Tekwani et al., 2013). Studies have shown that planktonic algae mainly originate from benthic algae via detaching from substrates due to flow abrasion, self-detachment processes and/or grazing by invertebrates (Swanson & Bachmann, 1976; Roeder, 1977; Tekwani et al., 2013). Similarly, planktonic algae may settle and attach to substrates when river flow is slow (Roeder, 1977; Tekwani et al., 2013). On the other hand, although planktonic and benthic algae occupy different habitats, they compete for abiotic resources, especially for light and nutrients (Hansson, 1988; Jäger & Diehl, 2014; Cardoso et al., 2019). Planktonic algae have the competitive advantage of light through reducing light transmission to benthic habitat while benthic algae have the advantage of nutrient utilization because they can absorb nutrients from both water volume and sediments (Hansson, 1990; Jäger & Diehl, 2014; Zhang & Mei, 2015).

Associations and differences between planktonic and benthic algae have substantial influence on community assembly processes. Numerous studies have shown that spatial patterns of algal assemblages are determined by both local environmental filtering and regional dispersal processes (Soininen, 2007; Smucker & Vis, 2011; Virtanen & Soininen, 2012; Liu et al., 2016), however, there is an ongoing debate regarding the relative contributions of these two processes. Four conceptual paradigms of metacommunity theory, including species sorting, mass effect, patch dynamics and neutral model, can integrate the local and regional factors (Leibold et al., 2004; Logue et al., 2011). According to this conceptual framework, planktonic and benthic algal assemblages may comply with different paradigms. Benthic algae may be more sensitive to local environmental conditions than planktonic algae because of their fixed habitats and more stable position (Battin et al., 2016; Chen et al., 2021). Thus, species sorting may serve as the main driver for shaping benthic algal assemblages. By comparison, planktonic algae with stronger dispersal ability can track local environmental variation, but are also strongly influenced by stochastic processes, such as directional flow, and can be washed into unsuitable habitats (Isabwe et al., 2018; Chen et al., 2021). Such temporary occurrence in suboptimal sites can be regarded as a signal of mass effect (Leboucher et al., 2020). However, only a few studies compared the differences in the community assembly processes of planktonic and benthic algal assemblages. Although several studies have discussed the issue in some large rivers, such as Negro River (Wetzel et al., 2012) and Yangtze River (Wang et al., 2019), they all treated algal dispersal as non-directional. But in fact, directional dispersal along river flow may be the most natural pathway for lotic algal dispersal across sites in a metacommunity (Kristiansen, 1996; Dong et al., 2016). Therefore, earlier studies may have underestimated the influence of the mass effect, especially in the wet season in large rivers, in which river communities may be

68   strongly affected by the mass effect, regardless of the local biotic and abiotic conditions (Heino et al., 2015b).

69   The relative importance of environmental and spatial processes on algal communities also may vary among seasons (Zhang

70   et al., 2019; Wang et al., 2020). Seasonal variation in river flow tends to change hydrological characteristics and trophic status in

71   the water bodies, and affects biotic community patterns, too (Biggs & Smith, 2002; Thomaz et al., 2007). In the wet season, many

72   algal taxa cannot survive due to intensive and frequent scour of flood and increased wetted area in the river channel and fast flow

73   may facilitate algal dispersal (Zhang et al., 2019; Li et al., 2020). Moreover, diffuse pollution is more likely to enter rivers through

74   surface runoff, thus affecting the composition of algal communities (Mao et al., 2018; Hu et al., 2020). By comparison, in the dry

75   season, lower flow is beneficial for sustaining stable algal communities, but also increases environmental heterogeneity and

76   reduces algal dispersal (Heino et al., 2015b; Zhang et al., 2019). Therefore, lotic algal assemblages may display season-specific

77   assembly processes (Heino et al., 2015b). Thus, comparing community assembly of organisms with different dispersal ability

78   (such as planktonic and benthic algae) may provide valuable insights into seasonal algal dynamics.

79   In the present study, we investigated biodiversity and assembly processes of planktonic and benthic diatom communities in

80   different seasons in the upper reach of the Jinsha River, in which diatoms represent the dominant algal group. The following three

81   hypotheses were tested: 1) planktonic and benthic diatom species richness and assemblage compositions will show seasonal

82   variation: the species richness of diatom assemblages decreases significantly in the summer, and planktonic and benthic diatom

83   assemblage compositions would be more similar in the summer due to flooding and associated strong dispersal; 2) planktonic

84   diatom assemblages are affected by directional spatial processes, suggesting mass effects while benthic diatom assemblages are

85   more affected by environmental filtering (species sorting); 3) directional spatial processes affect planktonic diatom assemblages

86   stronger in the summer, while environmental processes affect stronger benthic diatom assemblages in the autumn.

87

88   **Material and methods**

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90   Study area

91

92   The study area (97°14′~99°57′E, 26°53′~33°00′N) is located in Hengduan Mountains, a global biodiversity hotspot (Xing &

93   Ree, 2017). As the upstream of the Yangtze River, the largest river in China, the upper reach of the Jinsha River is 965 km long

94   and the catchment area is $2.6×10^5$ km^2. There are complex and diverse terrain types, deep river valleys, steep river banks and

95   substantial elevation gradient in the area and most sections of the river are inaccessible to humans. Therefore, the human

96   disturbance is relatively low in this area (Chen et al., 2020), but it also makes sample collection more difficult. The area is located

97   in the sub-tropical climate zone, and the land cover is mainly grassland, forestland and bare land with limited urbanization (Chen

98   et al., 2020). The rainfall mainly occurs in the summer (July to August), and mean precipitation is 392.76 mm in the summer and

99   144.98 mm in the autumn (Liu et al., 2016).

100   There is a lengthy winter (from October to April) in the upper reach of the Jinsha River after October, when roads are rough

101   and covered with snow and ice. Therefore, we conducted fieldwork in September of 2019 (autumn) and July of 2020 (summer).

102   Since the upper reach of the Jinsha River is not wadable, we sampled in the shallow water and involved different habitat types as

103   many as possible. We set up one sample site in every 50 km, with a total of 17 mainstream sites located in Qinghai, Sichuan and

104   Yunnan provinces surveyed, with elevation gradient from 1816 m to 3490 m (Fig. 1).

105

106   Diatom data

107   Planktonic diatom samples were collected in water column, while benthic diatom samples were collected on substrates.

108   Specifically, in each sampling occasion, 2 L of water were collected at each site for planktonic algae, and the samples were fixed

109   with neutral Lugol's solution immediately. After 48 hours of sedimentation, planktonic algal samples were concentrated to 50 ml

110   and stored with 4% formalin for further identification. At the same sites, in order to collect complete benthic algal communities,

111   different substrate types, including 15 stones or mud, were collected randomly from five spots along a 100 m reach. We used a

112   circular lid (radius: 2.7 cm) to fix the sampling area, and benthic algae were brushed into the specimen bottles. All subsamples

113   were pooled into one composite sample for each site and were preserved with 4% formalin in the field. In the laboratory, part of

114   diatom samples were acid-cleaned to make permanent diatom slides (Tang et al., 2016a). For each permanent diatom slide, at least

115   600 valves were identified and counted under a 1000× oil immersion lens. Diatoms were identified to species or variant level

116   based on taxonomic references of Hu & Wei (2006), Qi (1995), Shi (2004), Zhu (2007), Krammer (2000, 2002, 2003) and

117   Lange-Bertalot et al. (2001). The density and relative abundance were calculated for each taxon.

118   To estimate associations between planktonic and benthic diatom assemblages, each taxon in planktonic and benthic

119   assemblages was categorized to attached or unattached diatoms according to their attachment capacities. Attached diatoms are

120   firmly attached to substrates by different modes, while unattached ones float or freely move in water body (Heino & Soininen,

121   2006; Rimet & Bouchez, 2012). Based on Rimet & Bouchez (2012), adnate diatoms (e.g., *Cocconeis* spp.), diatoms attached by

122   mucilage pad (e.g., *Diatoma* spp.) and mucilage stalk (e.g., *Achnanthes* spp.) were classified as attached diatoms; and floating

123   (e.g., *Cyclotella* spp.) and free moving (e.g., *Navicula* spp.) diatoms were classified as unattached diatoms.

124

125   Environmental variables

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127   Physical and chemical variables were monitored at each sampling site. Elevation and geographical coordinates were

128   measured by GPS (Garmin Drive51). Current velocity (V) was measured with a LJD-10 velocity meter. Dissolved oxygen (DO),

129   pH, conductivity (Cond), turbidity (Turb) and water temperature (WT) were measured with a portable Yellow Springs Instrument

130   (YSI6600, USA). Additionally, 100 ml water sample was collected in an acid-proof bottle and sulfuric acid was added to regulate

131    $pH < 2$ in the field. After brought back to the laboratory, concentrations of chemical oxygen demand (COD), dissolved organic

132   carbon (DOC), silicate (SiO_2-Si), nitrate nitrogen (NO_3-N), ammonium nitrogen (NH_3-N), total nitrogen (TN), total phosphorus

133   (TP) and phosphate (PO_4-P) were measured by using a Skalar segmented flow analyzer (Skalar Analytical B.V., The Netherlands)

134   following the standard analysis procedures (Chinese NEPA, 2002).

135

136   Spatial variables

137

138   Considering that diatoms can spread between sites via various means, MEM (Moran's Eigenvector Map) and AEM

139   (Asymmetric Eigenvector Maps) were used to model dispersal processes of diatoms along geographical (overland dispersal) and

140   and network (dispersal along directional watercourse) pathways between sampling sites, respectively (Liu et al., 2013; Dong et al.,

141   2016). MEM is a spatial variable analysis model that does not consider directionality (Borcard & Legendre, 2002; Dray et al.,

142   2006). MEM variables showing positive eigenvectors based on geographical distances between sites were remained to model

143   spatial variables representing dispersal overland. In contrast, AEM is designed to model directional spatial processes (Blanchet et

144   al., 2011). Specifically, we first established a binary matrix of sites×edges through the geographical coordinate of sites and the

145   directional edges, then assigned weights to each edge. Weight was calculated as: Weight $= 1-(d/d_{\max})^2$, where d is watercourse

146   distances between sites, and $d_{\max}$ is maximum watercourse distances (Borcard et al., 2011). Finally, positive AEM eigenvectors

147   were generated and used as directional spatial predictors. Geographical distances between the sampling sites were calculated

148   based on the longitude and latitude data, the watercourse distances were calculated by using Network Analyst extension/OD Cost

149   Matrix tool in ArcGIS 10.0. MEM was carried out using function *pcnm* in R package 'vegan', AEM was computed using function

150   *aem* in R package 'AEM'.

151

152   Statistical analyses

153

154   Firstly, Mann-Whitney U test was used to examine the seasonal differences in diatom density and species richness and

155   environmental variables, and test whether there were significant differences between the relative abundance of attached and

156   unattached diatoms in diatom communities. Then, the percentage similarities (SIMPER) procedure was used to calculate the

157   contribution of individual species to the differences among different diatom assemblages. In addition, diatom community

158   composition was analyzed by Sørensen distance matrices based on presence-absence data. Specifically, Non-metric

159   Multidimensional Scaling (NMDS) was performed to analyze community dissimilarities among planktonic and benthic diatom

160   assemblages sampled from different seasons, and Permutational multivariate analysis of variance (PERMANOVA) was further

161   performed to test the significance for average differences between habitats (planktonic and benthic) and seasons (autumn and

162   summer) (Anderson, 2001). Then, NMDS and PERMANOVA were also used to perform same analysis to attached and unattached

163   diatom communities of planktonic and benthic assemblages.

164   Relative contributions of environmental and spatial variables on diatom assemblages were further analyzed using

165   distance-based redundancy analysis (db-RDA), which takes the distance matrix as the response variables based on redundancy

166   analysis. In the present study, diatom distance matrices based on Sørensen dissimilarity (i.e. β diversity) were used as the response

167 variables, and environmental variables and spatial predictors (MEM and AEM) as explanatory variables to perform db-RDA.

168 Before analysis, some environmental variables that had high correlation ($r > 0.8$) with other variables were removed. Then, in

169 order to simplify the model and eliminate collinearity between variables, a forward selection was used to identify significant

170 environmental and spatial variables. Forward selection processes were performed based on two stopping criteria: the adjusted

171 coefficient of determination (R^2_{adj}) of global model and alpha significance level ($P < 0.05$) (Blanchet et al., 2008). Finally,

172 variation partitioning analysis (VPA) was used to calculate the unique and shared effects of environmental and spatial variables

173 (Peres-Neto et al., 2006). Variation partitioning analysis has been widely used in recent studies because it can flexibly integrate the

174 effect of environmental models (local environmental factors) and different spatial models (e.g. dispersal models) (Dong et al.,

175 2016; Pozzobom et al., 2021).

176 　　All analyses were carried out in R (Version 3.6.3). Mann-Whitney U test was run by using 'stats' package, with package

177 'vegan' for NMDS, PERMANOVA, db-RDA, and variation partitioning using, and 'packfor' package for forward selection using.

178

179

180 **Results**

181

182 Seasonal variation in environmental variables

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184 　　Mann-Whitney U test showed that there were significant between-season differences in most environmental variables .

185 Turbidity, current velocity, dissolved organic carbon and water temperature were significantly higher in the summer; whereas total

186 phosphorus, phosphate, dissolved oxygen, pH and chemical oxygen demand had higher values in the autumn (Table1).

187

188 Associations and differences between planktonic and benthic diatoms

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190 　　A total of 122 planktonic and 111 benthic diatom species were observed in both seasons, with more benthic species

191 (planktonic vs benthic: 78: 93) in the autumn and more planktonic species (71: 52) in the summer (Fig.2). The number of species

192 appeared in both planktonic and benthic assemblages were 32 and 33 in the autumn and summer, with the shared proportions of

193 23.0% and 36.7%, respectively (Fig. 2). Considering attachment types for each diatom species, we found that in the summer, the

194 proportions of attached diatoms in planktonic and benthic assemblages decreased, while the proportions of unattached diatoms in

195 planktonic assemblages increased but in benthic assemblages decreased (Fig.2). The relative abundance of attached diatoms in

196 benthic assemblages was significantly higher than that of unattached diatoms in both seasons (autumn: $W = 289$, $P < 0.001$;

197 summer: $W = 233$, $P < 0.001$). As for planktonic assemblages, there was no significant difference between attached and unattached

198 diatoms for either seasons (autumn: $W = 107$, $P = 0.205$; summer: $W = 189$, $P = 0.131$) (Fig. 3).

199 　　*Achnanthidium minutissimum* was the predominant species that appeared in both types of diatom assemblages and both

seasons (Table 2). Besides, *Diatoma moniliformis* was dominant species (with mean relative abundance > 5%) in both planktonic and benthic assemblages in the autumn, and *Nitzschia dissipata* was dominant in benthic assemblages in both seasons. By comparison, other 13 dominant species only occurred in one diatom group or one season, including *Navicula accomoda*, *Navicula lanceolata* var. *phyllepta*, *Cyclotella caspia*, *Nitzschia palea*, *Fragilaria capucina*, *Navicula capitata* var. *hungarica*, *Navicula halophila*, *Denticula thermalis*, *Diatoma vulgaris*, *Cymbella minuta*, *Cocconeis placentula*, *Gomphonema olivaceum* and *Caloneis silicula* (Table 2). SIMPER analyses showed that the dominant species that occurred only in one group also tended to contribute most to the community dissimilarity between different habitats (benthic, planktonic) and seasons (autumn, summer) (Table 3).

Mann-Whitney U test showed algal density was significantly higher in the autumn than summer for both planktonic and benthic diatom communities. For species richness, only benthic diatoms in the autumn was higher than summer (Fig. 4).

NMDS combined with PERMANOVA revealed that community compositions between the two types of diatom assemblages differed significantly, but the differences between planktonic and benthic community compositions in the summer were smaller than that in the autumn (Fig. 5; Table S.1). Moreover, we carried out the same analysis (NMDS and PERMANOVA) of the attached and unattached communities of planktonic and benthic assemblages, and the results further confirmed there were smaller differences between planktonic and benthic community compositions in the summer than in the autumn. (see Supplementary Table S.1; Fig. S.1).

Relative contributions of environmental and spatial variables to diatom assemblages

Based on the results of forward selection procedure, DO was important for all diatom assemblages, but TN, Turb, pH and DOC were only selected for one diatom assemblage. For spatial variables, MEM1, MEM2 and AEM1 were selected for most assemblages, with MEM3, AEM5, AEM6 and AEM10 selected once (Table 4). Specifically, for planktonic assemblages, three environmental variables (TN, Turb and DO) and three spatial variables (MEM1, MEM2 and AEM1) were selected in the autumn, and one environmental variable (DO) and eight spatial variables (MEM1, MEM2, AEM1, AEM2, AEM3, AEM5, AEM6 and AEM10) were retained in the summer. For benthic assemblages, two environmental variables (TN and DO) and five spatial variables (MEM1, MEM2, AEM1, AEM2 and AEM3) were selected in the autumn, and four environmental variables (TN, DO, pH and DOC) and three spatial variables (MEM1, MEM3 and AEM1) were selected in the summer (Table 4).

For planktonic assemblages, both environmental and spatial processes were important in shaping diatom communities, but their contributions varied between seasons. In the autumn, spatial variables solely accounted for most variation (16.1%) in diatom communities, in which contribution of the MEM variables (11.1%) was higher than AEM variables (5.0%) (Fig. 6a), and environmental variables solely explained additional 14.2% of variation in diatom communities (Fig. 6a). In the summer, the unique effect of AEM variables was dominant, which explained 19.6% variation in diatom communities (Fig. 6b), whereas the unique effect of environmental variables was negligible. Moreover, the joint effects of environmental and spatial variables explained additional 10.2% and 19.3% variation in diatom assemblages in the autumn and summer, respectively (Fig. 6a, b).

233   For benthic assemblages, unique environmental effects were more important than spatial effects in both seasons.

234   Environmental variables independently accounted for 4.1% and 15.5% of variation in diatom assemblages in the autumn and

235   summer, respectively (Fig. 6c, d). By comparison, spatial variables independently accounted for less variation (0% and 2.3%) in

236   benthic assemblages. In addition, environmental and spatial variables jointly accounted for 25.7% and 7.9% of algal variation in

237   the autumn and summer, respectively (Fig. 6c,d).

238

239

240   **Discussion**

241

242   Associations and differences between planktonic and benthic diatom assemblages

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244   We found that the species richness of benthic diatoms decreased significantly in the summer, whereas there was no

245   significant difference between seasons in planktonic diatoms, which supported our hypothesis only in the benthic assemblages.

246   This result was understandable in such a large river because a large number of benthic diatoms might be scoured from their

247   habitats by strong flow in the summer (the average current velocity for the surveyed river reach was as high as 2.39 m/s in the

248   summer). In addition, extremely turbid river water in the summer (the average turbidity in the summer is 687.1 NTU) probably

249   limited benthic diatom growth. Conversely, the species diversity of planktonic assemblages did not decrease significantly in the

250   summer possibly due to input from detached benthic diatoms, or diatoms originating from upstream and tributaries (Améziane et

251   al., 2003; Tekwani et al., 2013). Thus, attached diatoms in benthic assemblages decreased while unattached diatoms in planktonic

252   diatoms increased in the summer. These findings point to the fact that attached and unattached diatoms might exchange frequently

253   between planktonic and benthic habitats due to water flow.

254   Our results showed that the community composition of planktonic and benthic assemblages differ in both seasons, suggesting

255   substantial difference in communities between different habitat types as found for other microorganisms, too (Feng et al., 2009;

256   Chen et al., 2021). This difference between planktonic and benthic communities relates to habitat preference of diatoms. We found

257   some species that were unable to firmly attach to the substratum, such as *Cyclotella caspia*, *Navicula accomoda*, *Navicula*

258   *capitata* var. *hungarica*, and *Nitzschia palea*, and become dominant taxa only in planktonic assemblages. However, some species

259   could firmly attach to substratum such as *Gomphonema olivaceum*, *Cymbella minuta*, *Cocconeis placentula* that were dominant

260   taxa only in benthic assemblages. These dominant species contributed most to differences among planktonic and benthic

261   assemblages. However, we also found some evidence that planktonic and benthic assemblages are coupled, especially in the

262   summer, which supported our hypothesis. For example, we found there were a considerable proportion of attached diatoms in

263   planktonic assemblages, such as *Achnanthidium minutissimum* and *Diatoma moniliformis*, which typically occur in benthic

264   assemblages. Our results also indicated that there was a larger proportion of shared species in the summer and the differences

265   between planktonic and benthic assemblages in the summer were relatively smaller than that of autumn. Indeed, it is likely that

266 benthic diatoms shift into planktonic phase in the summer during high flow conditions, resulting in more similar community

267 compositions in benthic and planktonic assemblages. It should be noted, however, that the interaction between planktonic and

268 benthic assemblages would be even better documented using more frequent field observations (e.g. daily sampling) instead of

269 admittedly temporally coarser sampling resolution used here (Tekwani et al., 2013).

270

271 Differences in community assembly processes between planktonic and benthic diatoms

272

273 Our results supported the hypothesis that planktonic diatoms were better dispersers passively and probably exhibited mass

274 effects given that planktonic assemblages were affected by directional spatial processes. Specifically, directional flow promotes

275 source-sink dynamics, causing species living in favorable habitats (sources) to disperse to unfavorable environments (sinks),

276 suggesting a signal of mass effect (Mouquet & Loreau, 2003; Leboucher et al., 2020). In addition to dispersal surplus (i.e. mass

277 effect), we found the non-directional spatial processes (i.e. MEM) were also important for planktonic diatom communities. In

278 fact, in the upper reach of Jinsha River, it could be expected that at large spatial extents   dispersal limitation probably prevents

279 diatoms to move between sites, thus causing considerable spatial signal in diatom assemblages. In addition, environmental factors

280 also played an important role for planktonic assemblages. This result was reasonable because the concept of the mass effect

281 suggests that the local environment is still critical for structuring biotic communities (Leibold et al., 2004; Brown & Swan, 2010).

282 Winegardner et al. (2012) further suggested that the mass effect is a special case of the species sorting when the dispersal rates are

283 very high. Therefore, local environmental processes should remain important when the dispersal rates are not too high, but in

284 contrast, if dispersal rates are high enough, mass effect could mask the effects of the environmental factors (Brown & Swan, 2010;

285 Heino et al., 2015a).

286 By comparison, we found that, the unique effects of environmental variables were more important than spatial variables for

287 the benthic assemblages, implying species sorting. Similar results emerged in earlier studies showing that environmental filtering

288 dominated the benthic algal community assembly (Soininen et al., 2016; Jamoneau et al., 2018; He et al., 2020). We found that

289 environmental filtering drove benthic diatom assemblages through physical and chemical factors, including TN, DO, pH and DOC.

290 These factors have been repeatedly recorded as important factors for algal communities (Biggs & Smith, 2002; Schönfelder et al.,

291 2002; Tang et al., 2013; Zorzal-Almeida et al., 2017). Moreover, we should also note that the joint effect of environmental and

292 spatial variables explained considerable variation of benthic assemblages. This may reflect the fact that covariation of

293 environmental variables along geographical space masked some unique environmental effects. For example, we found that some

294 environmental variables selected through forward selection, such as DO, TN, significantly varied along the geographical distance,

295 thus partly revealing such covariation (see Supplementary Fig. S2). In addition, the use of spatial eigenvectors may also lead to

296 the underestimation of the influence of pure environmental factors (Gilbert & Bennett, 2010). Other studies also reported such

297 joint effect and suggested this fraction is difficult to explain from the perspective of ecological mechanisms because the effects of

298 environment and space cannot be separated easily due to their covariation in nature (Cottenie, 2005; Vilmi et al., 2016; Keck et al.,

299   2018). Overall, although the joint effect is unavoidable, our results still supported the importance of environmental filtering on

300   benthic diatom assemblages, because unique effects of environmental processes override spatial processes.

301   It should be noted that the total unexplained variations of diatom communities were relatively high (from 58.7% to 66.5%),

302   but such high proportions have been found in many related studies using variance partitioning (Vilmi et al., 2016; Li et al., 2020;

303   Pozzobom et al., 2021). It may be due to the fact that many potential variables affecting biotic communities cannot be adequately

304   measured, such as abiotic factors (e.g., runoff   and slope), biotic variables (e.g., intraspecific and interspecific competition),

305   neutral processes (e.g., colonization and extinction) and historical effects (e.g. climatic history) (Göthe et al., 2013; Benito et al.,

306   2018; Li et al., 2020). In addition, sampling difficulties in our study area probably also increased the unexplained variations.

307

308   Effects of seasonal dynamics on diatom community assembly

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310   Although our results showed that mass effect and species sorting were explaining the assembly processes of planktonic and

311   benthic diatom assemblages, respectively, the explanatory powers of these two paradigms were seasonally variable. One reason

312   for this difference was seasonally changing flow rates, which may alter the relative importance of environmental and spatial

313   processes (Li et al., 2020; Wang et al., 2020). We found the effects of directional dispersal on planktonic were more important in

314   the summer, which supported our hypothesis. Diatoms in planktonic assemblages as better passive dispersers were more easily

315   affected by changing flow rates (Isabwe et al., 2018), and therefore, as river flow was higher and faster in the summer, directional

316   dispersal made planktonic assemblages to show stronger source-sink effect (i.e. mass effect). In contrast, as river flow was

317   relatively low in the autumn, the effects of directional dispersal decreased. However, our results did not fully support our

318   hypothesis because we found environmental processes to be more important to benthic assemblages in the summer. This finding

319   suggested that although many diatoms in the benthic assemblages were scoured from their habitats, there were still some diatoms

320   that firmly attached to substrates, especially some dominant taxa that indicate changing environmental conditions in the summer.

321   In general, our results emphasized the importance of seasonal dynamics on diatom community assembly, but in the same time, the

322   complexity of this process makes it difficult to be understood when considering solely either dispersal or environmental filtering.

323   Therefore, we advocate the consideration of multiple metacommunity processes to better understand stream seasonal dynamics.

324

325   Potential applications

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327   There is an ongoing discussion on using planktonic or benthic diatoms to assess ecological conditions of streams and rivers

328   (Kireta et al., 2012). Most studies on streams and wadable rivers have considered benthic diatoms because plankton is rare in such

329   systems (Tang et al., 2016b; Pajunen et al., 2020). However, as planktonic and benthic algae seem to coexist in many rivers, our

330   results may provide valuable information for such selection on which group to target the research efforts. Compared with

331   planktonic algae, we found that community assembly of benthic diatoms were stronger attributed to local environmental

conditions than dispersal processes. For ecological assessments, we need indicators that can reflect local environmental variation between sites effectively and are not sensitive to spatial factors, which is especially important when assessment is performed across extensive geographical areas (Soininen et al., 2004; Soininen, 2007; Vilmi et al., 2016). Therefore, benthic diatoms are better indicators for bioassessment. By comparison, high dispersal rates due to directional spatial processes make planktonic communities highly stochastic, and increases the uncertainties when used as bioindicators (Vilmi et al., 2016).

In conclusion, our study showed both associations and differences in biodiversity and assembly processes of planktonic and benthic diatom assemblages in a large subtropical river. Generally, we found that species richness and community composition of planktonic and benthic diatom assemblages show different seasonal variation due to their different dispersal ability and habitat preference. High flow conditions in the summer influenced the diatom diversity and promoted more similar community compositions in benthic and planktonic assemblages. For community assembly processes, we found directional spatial processes to dominate the assembly processes of planktonic diatom assemblages especially in the summer, suggesting a signal of mass effect; the effects of environmental processes vary among changing flow rates in the autumn and summer. By comparison, benthic diatom assemblages were mainly determined by environmental filtering. Our study thus suggested mass effect and species sorting are suitable for explaining the assembly processes of planktonic and benthic diatom assemblages, respectively, but the explanatory powers vary among different seasons. Giving that benthic diatoms better resist directional flow disturbance and reflect local environmental conditions than planktonic diatoms, we recommend using benthic diatoms to indicate river environmental conditions in future ecological assessment programs.

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522 **Table 1** Seasonal variation in environmental variables in the upper reach of the Jinsha River.

Environmental variables	Abbreviation	Autumn	Summer	P
		Mean (Range)	Mean (Range)	
Total nitrogen (mg/L)	TN	0.64 (0.30~0.84)	0.63 (0.42~0.88)	0.77
Nitrate nitrogen (mg/L)	NO_3-N	0.51 (0.21~0.64)	0.44 (0.20~0.67)	0.08
Ammonia nitrogen (mg/L)	NH_3-N	0.07 (0.02~0.17)	0.08 (0.03~0.15)	0.41
Total phosphorus (mg/L)	TP	0.17 (0.06~0.24)	0.08 (0.02~0.29)	**<0.01**
Phosphate (mg/L)	PO_4-P	0.14 (0.05~0.22)	0.07 (0.02~0.24)	**<0.01**
Conductivity (mg/L)	Cond	596.2 (153.8~766.0)	460.7 (102.6~990.0)	0.09
Silicate (mg/L)	SiO_2-Si	6.08 (3.81~8.06)	6.18 (3.93~10.09)	0.86
Dissolved Oxygen (mg/L)	DO	8.69 (8.05~9.38)	7.90 (6.79~9.30)	**<0.001**
Dissolved organic carbon (mg/L)	DOC	1.14 (0.71~2.51)	2.43 (1.68~3.41)	**<0.001**
Chemical oxygen demand (mg/L)	COD	2.91 (0.89~4.50)	1.14 (0.69~1.51)	**<0.001**
pH	pH	8.35 (8.28~8.50)	8.13 (7.90~8.60)	**<0.001**
Turbidity (NTU)	Turb	366.4 (33.8~482.0)	687.1 (85.8~1042.3)	**<0.001**
water temperature (°C)	WT	11.25 (8.50~14.30)	15.58 (12.90~17.20)	**<0.001**
Current velocity (m/s)	V	0.40 (0.10~0.94)	2.39 (0.9~3.7)	**<0.001**

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544 **Table 2** Diatom taxa with mean relative abundance (%) > 5% in planktonic and benthic diatom communities in the upper reach of

545 the Jinsha River

Taxa	Planktonic		Benthic	
	Autumn	Summer	Autumn	Summer
Achnanthidium minutissima	10.03	12.22	24.34	18.33
Caloneis silicula				5.36
Cocconeis placentula				8.20
Cyclotella caspia	7.58			
Cymbella minuta			6.42	
Denticula thermalis		5.68		
Diatoma moniliformis	6.26		5.04	
Diatoma vulgaris		5.17		
Fragilaria capucina		15.38		
Navicula accomoda	9.06			
Navicula capitata var. *hungarica*		6.03		
Navicula halophila		5.90		
Navicula lanceolata var. *phyllepta*	8.71			
Nitzschia palea	6.77			
Gomphonema olivaceum				6.27
Nitzschia dissipata			5.89	7.14

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564 **Table 3** Average contributions (%) of particular species to diatom community dissimilarity between different habitats
565 (benthic, planktonic) and seasons (autumn, summer) using SIMPER (similarity percentages) analysis.

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Species	Autumn VS Summer		Planktonic VS Benthic	
	Planktonic	Benthic	Autumn	Summer
Fragilaria capucina	7.69			6.90
Achnanthidium minutissima	5.67	9.86	8.08	8.70
Navicula accomoda	4.52		4.48	
Navicula lanceolata var. *phyllepta*	4.35		4.38	
Cyclotella caspia	3.49		3.76	
Diatoma moniliformis	3.15		3.54	
Navicula capitata var.*hungarica*	3.01			3.01
Cocconeis placentula		4.03		4.01
Nitzschia dissipata		3.77		3.19
Cymbella affinis		3.04		
Navicula oblonga				3.81
Gomphonema olivaceum				3.09
Other species	55.0	54.0	58.2	48.3

571 **Table 4** Environmental and spatial variables selected by forward selection for explaining variation in planktonic and benthic
572 diatom communities

Taxa	Season	Variable		
		ENV	MEM	AEM
Planktonic	Autumn	TN	MEM1	AEM1
		Turb	MEM2	
		DO		
	Summer	DO	MEM1	AEM1
			MEM2	AEM2
				AEM3
				AEM5
				AEM6
				AEM10
Benthic	Autumn	TN	MEM1	AEM1
		DO	MEM2	AEM2
				AEM3
	Summer	TN	MEM1	AEM1
		DO	MEM3	
		pH		
		DOC		

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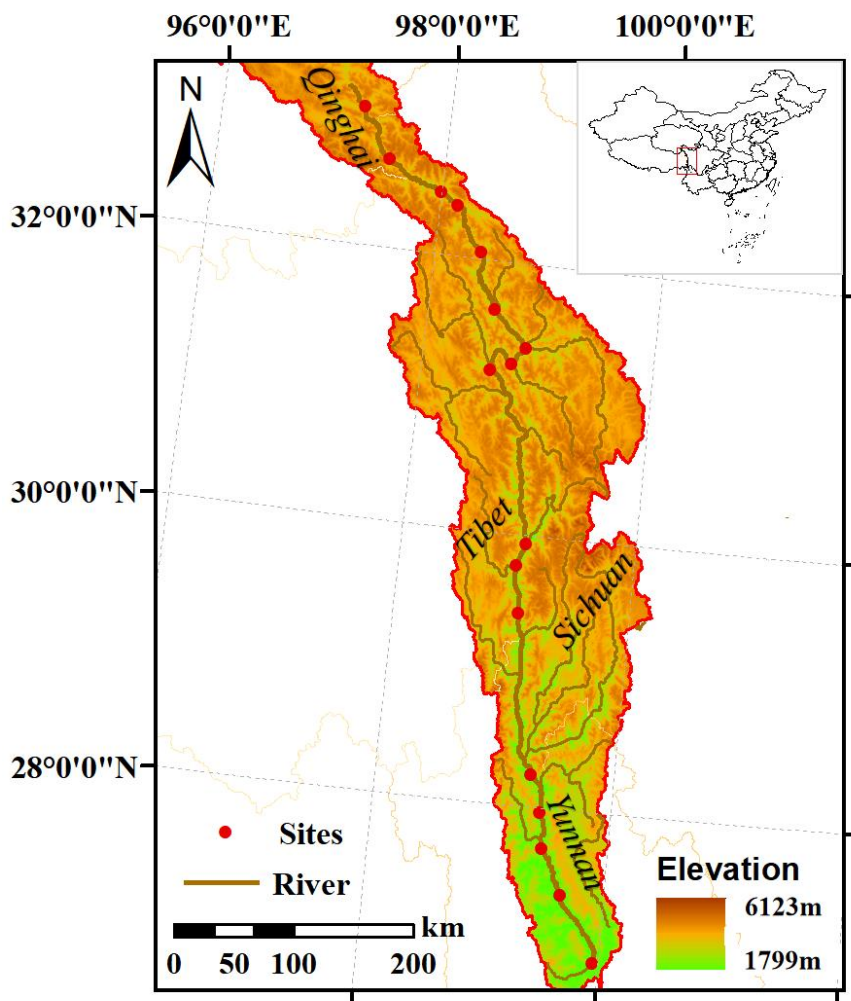
588　　　　　　　　　　　**Fig. 1** Locations the sampling sites in the upper reach of the Jinsha River, China

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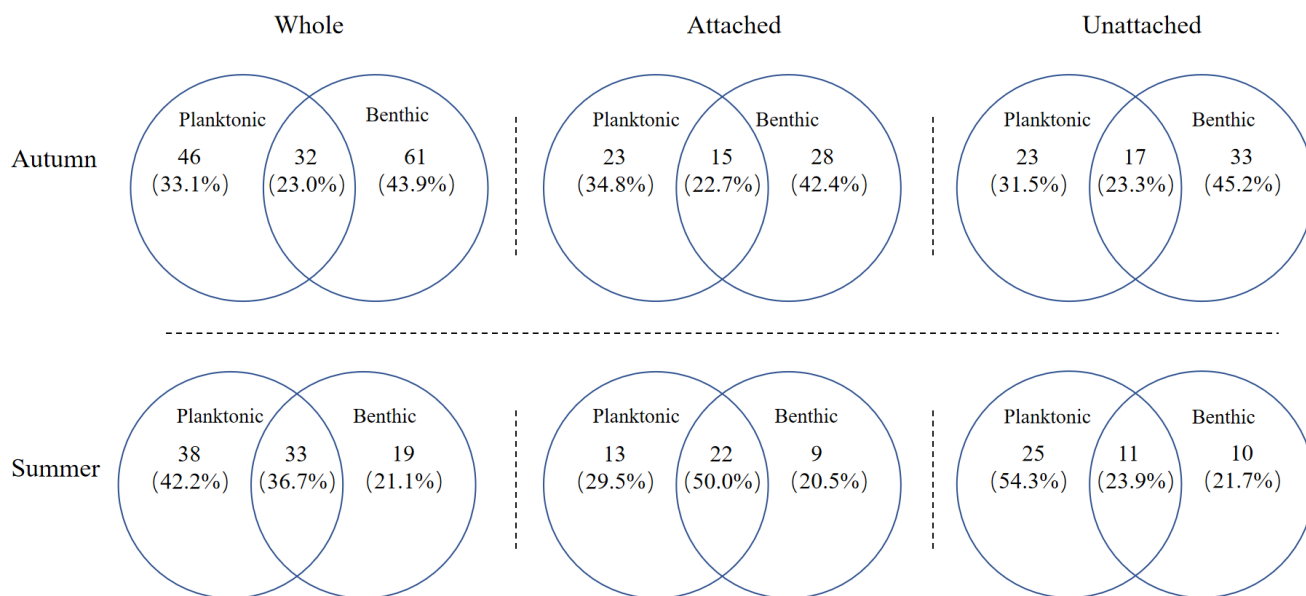
Fig. 2 The Venn diagram showing the number of individual and shared species (their percentages are presented in parentheses) appearing in the whole, attached and unattached communities of planktonic and benthic diatom communities in the autumn and summer
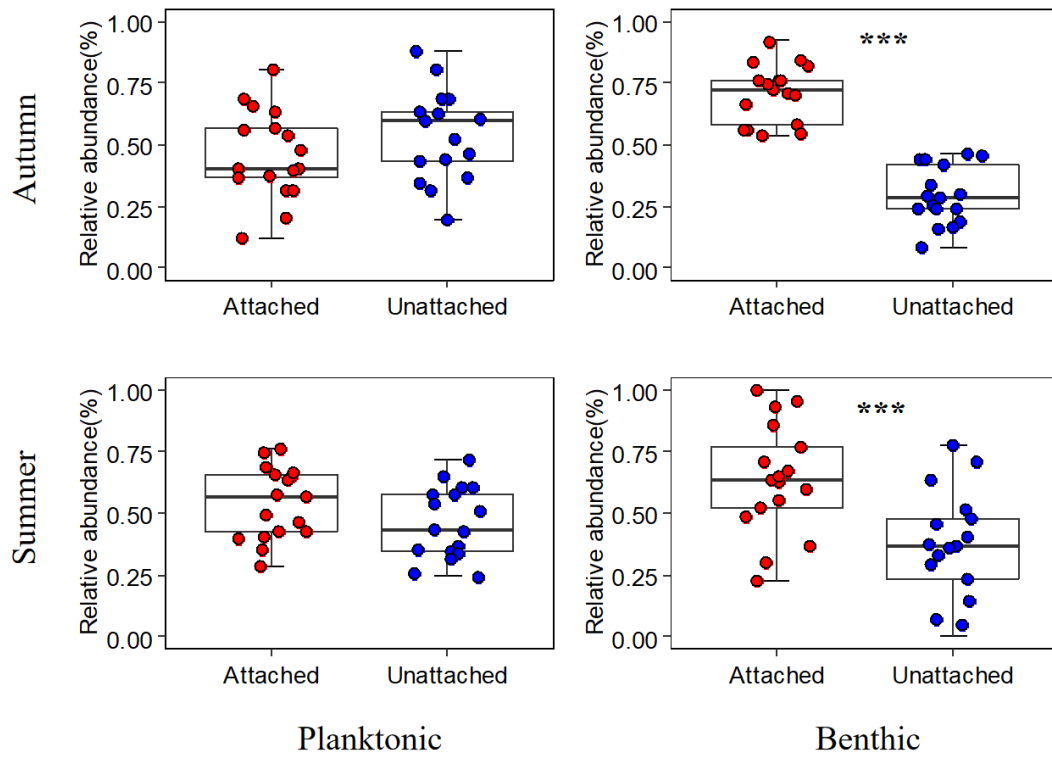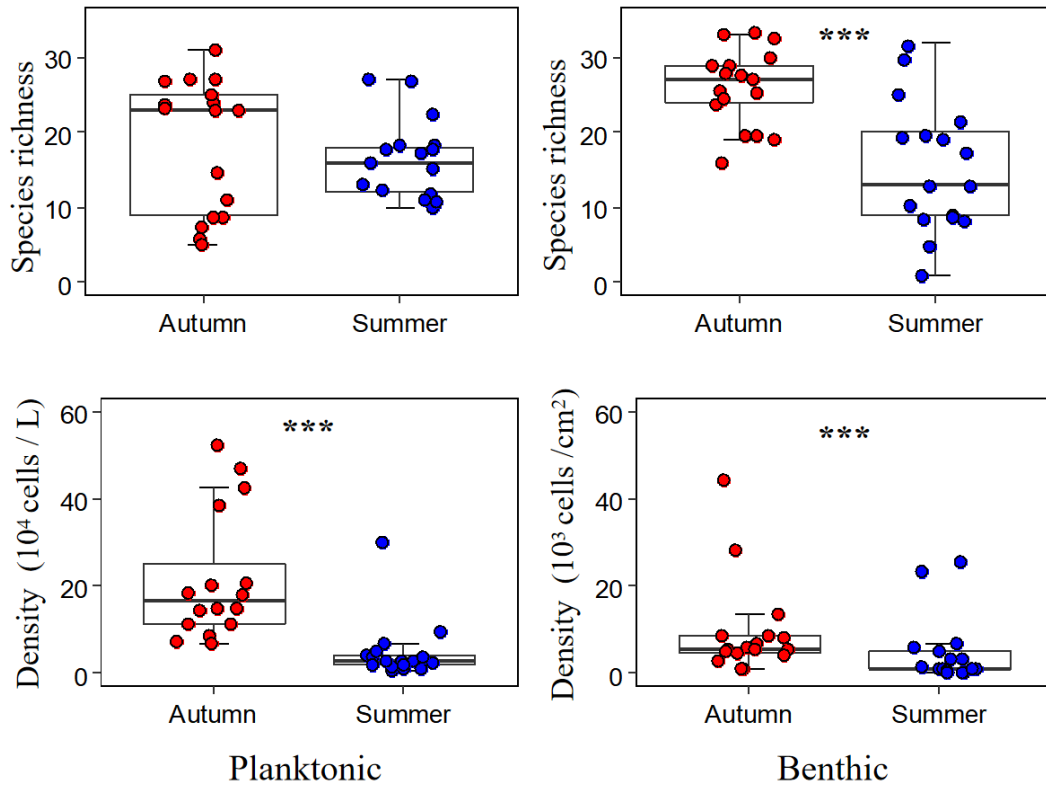
Fig. 3 Boxplots displaying value ranges of relative abundances of attached and unattached diatoms observed in planktonic and benthic communities in the autumn and summer. *** indicates significant difference ($P < 0.001$) with Mann-Whitney U test

Fig.4 Comparison of seasonal differences of species richness and density between planktonic and benthic diatom communities. As

*** represent significant difference ($P < 0.001$)
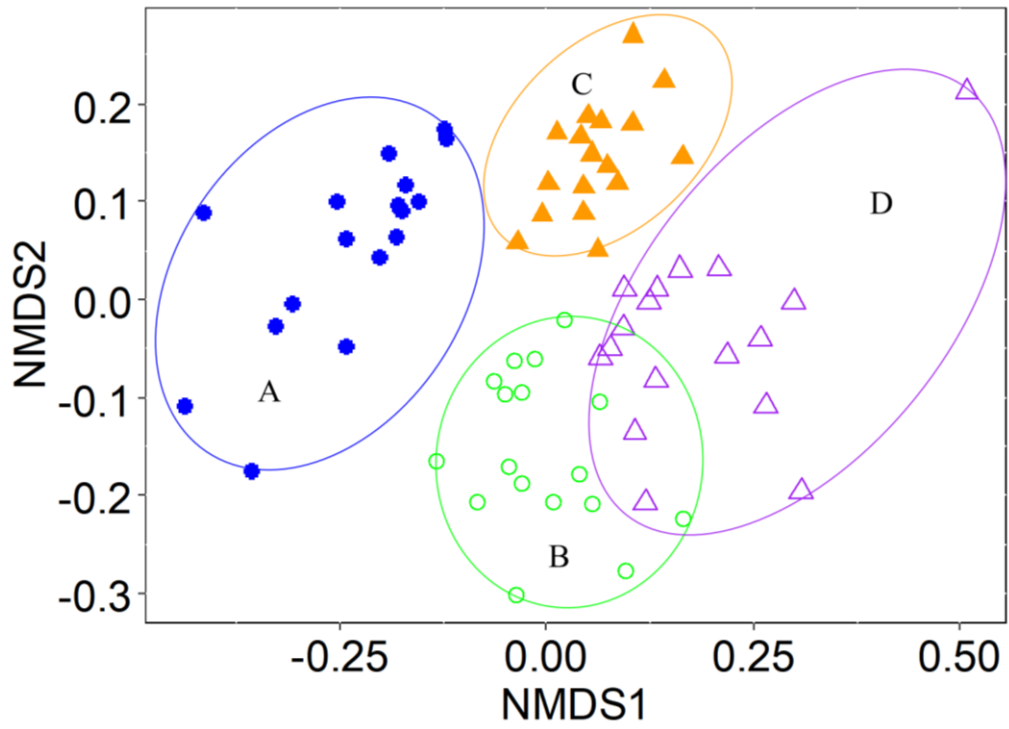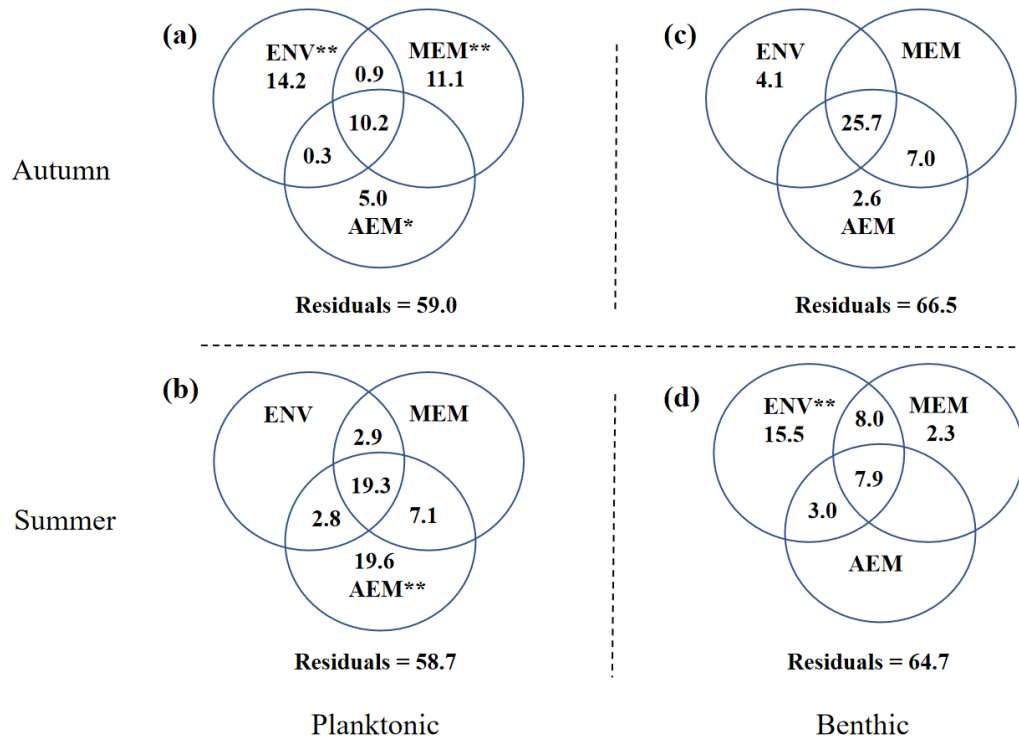
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Fig. 5 Non-metric multidimensional scaling diagram (NMDS) showing community dissimilarities among planktonic and benthic diatoms in the autumn and summer. A: planktonic diatom communities in the autumn; B: planktonic diatom communities in the summer; C: benthic diatom communities in the autumn; D: benthic diatom communities in the summer

(a) Autumn

ENV** 14.2 · 0.9 · MEM** 11.1 · 10.2 · 0.3 · 5.0 AEM*

Residuals = 59.0

(c)

ENV 4.1 · MEM · 25.7 · 7.0 · 2.6 AEM

Residuals = 66.5

(b) Summer

ENV · 2.9 · MEM · 19.3 · 2.8 · 7.1 · 19.6 AEM**

Residuals = 58.7

(d)

ENV** 15.5 · 8.0 · MEM 2.3 · 7.9 · 3.0 · AEM

Residuals = 64.7

Planktonic · Benthic

Fig. 6 The Venn diagram showing the unique and shared contributions of environmental variables (ENV) and spatial variables (MEM, AEM) to (a) planktonic diatom communities in the autumn, (b) planktonic diatom communities in the summer, (c) benthic diatom communities in the autumn, (d) benthic diatom communities in the summer. Values < 0 are not shown and residuals represent unexplained fractions. * indicate significance, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$