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1 **Environmental filtering and spatial effects on metacommunity**  
2 **organisation differ among littoral macroinvertebrate groups**  
3 **deconstructed by biological traits**

4  
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21  
22 **Abstract**

23 We examined spatial and environmental effects on the deconstructed assemblages of littoral macroinvertebrates  
24 within a large lake. We deconstructed assemblages by three biological trait groups: body size, dispersal mode  
25 and oviposition behaviour. We expected that spatial effects on assemblage structuring decrease and  
26 environmental effects increase with increasing body size. We also expected stronger environmental filtering  
27 and weaker spatial effect on the assemblages of flying species compared with assemblages of non-flying  
28 species. Stronger effect of environmental filtering was expected on the assemblages with species attaching eggs  
29 compared with assemblages of species with free eggs. We used redundancy analysis with variation partitioning  
30 to examine spatial and environmental effects on the deconstructed assemblages. As expected, the importance of  
31 environmental filtering increased and that of spatial effects decreased with increasing body size. Opposite to  
32 our expectations, assemblages of non-flying species were more affected by environmental conditions compared  
33 to assemblages of flying species. Concurring with our expectations, the importance of environmental filtering  
34 was higher in structuring assemblages of species attaching eggs than in structuring those with freely-laid eggs.  
35 The amount of unexplained variation was higher for assemblages with small-sized to medium-sized species,  
36 flying species and species with free eggs than those with large-sized species, non-flying species and species  
37 with attached eggs. Our observations of decreasing spatial and increasing environmental effects with increasing  
38 body size of assemblages deviated from the results of previous studies. These results suggest differing  
39 metacommunity dynamics between within-lake and among-lake levels and between studies covering  
40 contrasting taxonomic groups and body size ranges.

41 **Keywords** Metacommunity organisation · Niche width · Biological traits · Large lakes

## 42 **Abstract**

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61 groups and body size ranges.

62

## 63 **Introduction**

64 According to the metacommunity perspective, local communities are structured by the interplay between  
65 local environmental conditions and regional processes (Leibold et al. 2004), such as the intensity of dispersal  
66 between habitat patches and possible barriers for dispersal (Logue et al. 2011; Heino et al. 2015). Recently,  
67 metacommunity theory has become the dominant framework through which ecologists examine the  
68 structuring of biological communities (Brown et al. 2017). The four major paradigms of metacommunity

69 ecology, i.e. species sorting through the process of environmental filtering (Leibold 1998), mass effects  
70 (Mouquet and Loreau 2002; 2003), neutrality (Hubbell 2001) and patch dynamics (Tilman 1994), are  
71 examples emphasizing some of the controlling factors of metacommunity dynamics (Logue et al. 2011;  
72 Brown et al. 2017). However, these paradigms fail to recognize the continuous and multidimensional nature  
73 of metacommunity dynamics (Brown et al. 2017). More recent views of metacommunity dynamics  
74 recognize, however, that dispersal and environmental filtering are not mutually exclusive (Gravel et al. 2006;  
75 Logue et al. 2011), and emphasize that dispersal and local environmental conditions simultaneously affect  
76 the structure of local communities. For example, adequate amount of dispersal is needed to enable species  
77 sorting through environmental filtering, whereas low dispersal rates result in increased effect of dispersal  
78 limitation on community assembly and high dispersal rates to the dominance of mass effects (Winegardner et  
79 al. 2012; Heino et al. 2015; Brown et al. 2017).

80

81 Biological traits are characteristics that relate to the environmental responses, dispersal and competitive  
82 abilities of species (McGill et al. 2006). Therefore, biological traits are keys to understand metapopulation  
83 and metacommunity dynamics, i.e. the responses of individual species and entire biotic communities to  
84 spatial processes and local environmental conditions (De Bie et al. 2012; Heino 2013). A suitable model  
85 group for examining trait-environment relationships by community deconstruction are littoral  
86 macroinvertebrates. This is because littoral macroinvertebrates show a diverse suite of biological traits  
87 related to feeding mode, substrate attachment, oviposition behaviour, body size, dispersal mode and dispersal  
88 abilities (Hanna 1961; Pinder 1995; Tolonen et al. 2003; Heino 2008; Heino and Tolonen 2017; Tolonen et  
89 al. 2017). For example, body size has been recognized as one of the key traits that may determine  
90 metacommunity structure because it is expected to be related to dispersal ability (De Bie et al. 2012).  
91 Generally, in larger spatial scale and among-lake studies, the effect of spatial processes in structuring  
92 communities increases and effect of local environmental conditions decreases with increasing body size of  
93 organisms (De Bie et al. 2012; Soininen 2016). However, these expectations of metacommunity structuring-  
94 species traits relationships may be different in highly-connected systems, such as a single large lake, and  
95 within a single ecological group, such as littoral macroinvertebrates. The dispersal mode of organisms has a  
96 key role in determining how species are spatially distributed and how they are interacting with their

97 environment (Cottenie 2005). Passive dispersers (e.g. worms, clams and mussels) are dispersed by water  
98 currents or by larger animals (Bilton et al. 2001; Vanschoenwinkel et al. 2008), and they may have limited  
99 ability to actively select their habitats (Vanschoenwinkel et al. 2008). Active dispersers (e.g. flying insects)  
100 can actively select their habitats and oviposition sites to ensure favourable environmental condition for their  
101 offspring (Berendonk 1999; Resetarits 2001). Aerial dispersal is generally the most important mode of  
102 dispersal among lake littoral macroinvertebrates, and often the majority of species and individuals in  
103 macroinvertebrate communities consist of aquatic insects with flying adults (e.g. 56-61 % of abundance in  
104 Tolonen et al. 2001; Tolonen and Hämäläinen 2010). In addition to dispersal modes, divergent oviposition  
105 behaviours of freshwater macroinvertebrate species constitute important life history strategies (Verberk et al.  
106 2008) that may also be related to community assembly (Heino and Peckarsky 2014). Many  
107 macroinvertebrate species attach their eggs selectively on solid substrates, such as on aquatic plants or on  
108 stones below water surface. Another common oviposition strategy is to lay eggs freely on water surface  
109 (Hanna 1961; Pinder 1995). Therefore, water currents within a lake may have important effects on the  
110 dispersal of some aquatic insect taxa (e.g. non-biting midges) due to the planktonic behaviour of their eggs  
111 (laid freely to the water surface) and first instar larvae (Davies 1976; Pinder 1995).

112

113 In this study, we examined the effects of local environmental conditions and spatial processes on the  
114 metacommunity organisation of littoral macroinvertebrates in a large lake system through deconstructing  
115 entire assemblages by biological trait groups. These traits included: (1) body size (small-, medium-, and  
116 large-sized), (2) dispersal mode (non-flying and flying), and (3) oviposition behaviour (free oviposition on  
117 water surface and selective oviposition on solid surfaces). Earlier across-taxonomic group, among-lake (De  
118 Bie et al. 2012) and larger spatial-scale studies (Soininen 2014; 2016) have indicated that spatial effects  
119 increase and environmental effects decrease with increasing body size of species in biotic assemblages.  
120 Opposite to these studies, we expected that, with increasing macroinvertebrate body size, the importance of  
121 environmental filtering increases and spatial processes decreases within a single lake system (Table 1). This  
122 is because the dispersal capacity of active dispersers has been observed to be positively correlated with body  
123 size (Jenkins et al. 2007) and, among flying aquatic insects, large species are generally stronger flyers than  
124 small ones (Compton 2002; Hoffsten 2004). Large-sized flying species are considered stronger dispersers

125 and may be more able to move in an optimal (desired) direction in windy pelagic zones of large lakes (see  
126 Compton 2002; Rundle et al. 2007). Therefore, large species may be more effective in selecting oviposition  
127 sites and, hence, finding optimal habitats for their offspring when compared to small-sized species.  
128

129 Dispersal mode is also considered to be one of the chief factors affecting metacommunity dynamics  
130 (Cottenie 2005; De Bie et al. 2012). The examinations of multiple taxonomic groups across large spatial  
131 scales have indicated that passive dispersers are mainly controlled by environmental conditions with minor  
132 effects of spatial processes, whereas the assemblages of actively flying dispersers are more equally structured  
133 by environmental and spatial effects (Cottenie 2005; De Bie et al. 2012). However, among-lake studies  
134 comparing flying and passive dispersers with approximately equal sizes indicated that flying dispersers may  
135 be relatively more controlled by local environmental conditions than passive dispersers, whereas spatial  
136 effects may be stronger on passive dispersers with aquatic adult stages than on flying dispersers (De Bie  
137 2012; Heino 2013). Therefore, we expected that the effects of spatial processes are stronger on non-flying  
138 (passive dispersers) than on flying species (active dispersers) in our highly-connected large lake system  
139 (Table 1). An opposite relationship is expected for the effect of local environmental conditions on the  
140 assemblage structure of dispersal mode groups, with there being a stronger effect on assemblages of flying  
141 species than on those of non-flying species.  
142

143 Finally, oviposition mode (free or attached eggs) may also be among the key factors determining the  
144 organisation of lake macroinvertebrate metacommunities. Slowly sinking, drifting eggs and egg masses laid  
145 freely on the water surface may disperse long distances with water currents (Davies 1976). Directions of  
146 surface water currents in lakes are changing with changes in wind directions (Huttula et al. 1996; Ji et al.  
147 2002; Schernewski et al. 2005; Wu et al. 2016), and water currents have been observed to influence the  
148 distribution patterns of planktonic organisms in lakes (Ji et al. 2002; Schernewski et al. 2005). Therefore,  
149 relatively larger roles of random effects (unexplained variation) can be expected in the assemblages laying  
150 their eggs freely compared to the assemblages attaching their eggs (Table 1). We also expected that attaching  
151 eggs selectively on solid substrates should increase the importance of environmental filtering when  
152 compared to the oviposition behaviour with eggs laid freely on the water surface.

153

## 154 **Material and methods**

### 155 Sampling and identification of macroinvertebrates

156 In September 2013, littoral macroinvertebrates were sampled at 70 stony bottom sites, which covered all sub-  
157 basins and were located evenly around the entire perimeter of the Kitkajärvi lake system (surface area 305  
158 km<sup>2</sup>) in northeastern Finland (centered on 66°10'N, 028°39'E) (Fig. 1). Macroinvertebrates were sampled  
159 using a kick-net with 0.5 mm mesh-size. At each site, a pooled sample of six kicks, each along a 1-m stretch  
160 for 30 s, were taken at 20 to 50 cm depth. This represented 6 m and 3 minutes sample size in total. When  
161 taking each of the 30 second subsample, the field worker moved backwards and simultaneously kicked the  
162 substrate, and moved the net from side-to-side close to the bottom. Samples were sieved using 0.5 mm mesh  
163 and preserved in ethanol in the field. In the laboratory, the samples were sorted and animals were counted  
164 and identified usually to species or genus, including the species-rich family Chironomidae. However, for the  
165 Oligochaeta, only a few common taxa were identified to species level. Water mites (Hydracarina) were not  
166 identified to lower taxonomic levels. All the work phases in field and laboratory were conducted by the same  
167 persons.

168

### 169 Measurements of local environmental variables

170 Wind fetch (m) of each site was calculated using ArcGIS-based analysis tool (Rohweder et al. 2008). Bottom  
171 slope (%) was calculated between the depths of 0.5 and 2 metres based on the site-specific distance  
172 measurements. Coverage (%) of substratum particle sizes was visually assessed following modified  
173 Wentworth classes: organic substratum (mud and leaf litter), fine inorganic sediment ( $\leq 2$  mm), gravel (2-  
174 16 mm), pebble (16-64 mm), cobble (64-256 mm), boulders (256-1024 mm), large boulders (> 1024 mm)  
175 and bedrock. The mean substratum particle size (SPS) was calculated as a weighted mean of the midpoints of  
176 the substratum size categories (e.g. 160 mm for the cobble 64-256 mm). Substratum particle diversity (SPD)  
177 was calculated using Shannon diversity index (Shannon 1948). Samples for physical and chemical properties  
178 of water were taken and analysed according to national standard methods (Finnish Standards Association

179 SFS), which are consistent with the pan-European standards (CEN, the European Committee for  
180 Standardization). Altogether 35 water chemistry variables were analysed from water samples taken at each  
181 sampling site (Supplementary Material Table S1).  
182  
183 Epilithic algal biomass (ELA BM) ( $\text{chl-}a \mu\text{g cm}^{-2}$ ) was measured using *in vivo* fluorescence measurements  
184 by BenthosTorch portable benthic algae analyser ([www.bbe-moldaenke.de/chlorophyll/benthosTorch](http://www.bbe-moldaenke.de/chlorophyll/benthosTorch)). Ten  
185 randomly selected stones were collected from the depth of 40 cm for BenthosTorch measurements at each  
186 site. Total surface area of the algal measurements was  $9.6 \text{ cm}^2$ . At each site, fish biomass was estimated by  
187 electrofishing without escape nets. Fish were sampled once from  $100 \text{ m}^2$  area at each site (Sutela et al. 2016).  
188 Percentage (%) coverage of macrophytes was estimated from six  $1 \text{ m} \times 1 \text{ m}$  plots positioned randomly to the  
189 depths of 0-2 m along the transect perpendicular to the shoreline.

190  
191 Many of the environmental variables measured were strongly correlated ( $r > 0.6$ ). Therefore, to avoid  
192 interpretation problems related to multicollinearity, we selected only one variable (considered to be  
193 ecologically most influential) among each set of correlated parameters to be used in subsequent statistical  
194 analyses. This selection procedure resulted in a set of 17 uncorrelated environmental explanatory variables  
195 (Table 2).

196

## 197 Spatial variables

198 Principal coordinates of neighbour matrix analysis (PCNM, Borcard and Legendre 2002) was conducted to  
199 produce spatial eigenvectors for the analyses of spatial structures in the littoral macroinvertebrate species  
200 composition. PCNM uses geographic (x and y) coordinates taking into account complex spatial structures,  
201 including those that are nonlinear and occur at multiple spatial scales (Borcard and Legendre 2002). PCNM  
202 analysis was conducted using the R package PCNM (Legendre et al. 2013). The analysis using coordinates  
203 of the 70 sampling sites resulted in 27 PCNM eigenvectors showing positive spatial autocorrelation. These  
204 eigenvectors were used as explanatory spatial variables in further analyses. First (V1, V2, V3, etc.) spatial  
205 variables represented large-scale and last (V27, V26, V25, etc.) small-scale spatial relationships among the



206 sampling sites. Current nomenclature connects PCNM analysis to the framework of Moran's eigenvector  
207 maps, and PCNM eigenvectors are thus nowadays also called distance-based Moran's eigenvector maps  
208 (dbMEM) (Dray et al. 2012).

209

## 210 Classification of biological traits

211 Singletons, i.e. species found only in one sampling site, were excluded from the biological trait  
212 classifications and further statistical analyses, since biological trait classifications were missing for many of  
213 these rare species. After removing singletons, 112 species remained for statistical analyses. Biological trait  
214 groups studied were body size, dispersal mode and oviposition behaviour. Body size of each species was  
215 calculated based on length-weight relationships obtained from the literature, and were reported as a mean  
216 potential maximum size of aquatic stages (see Tolonen et al. 2017). Species were then ranked from the  
217 smallest to the largest, and divided into three groups with approximately equal number of species in each:  
218 small-sized, medium-sized and large-sized species. Species were also classified into the groups of active  
219 dispersers of flying insects and passive dispersers of non-flying species. Furthermore, species were classified  
220 into two groups based on their oviposition behaviour: species laying slowly sinking "planktonic" eggs on the  
221 water surface (free eggs), and species laying and attaching their eggs selectively on solid surfaces (e.g.  
222 macrophytes and benthic substrates). Species-specific classifications of biological traits with their literature  
223 references are given in the Supplementary Material Table S2.

224

## 225 Modelling variation in assemblage structure

226 First, to examine overall dissimilarity within each deconstructed assemblage i.e. assemblage variation based  
227 on abundance data, we calculated Bray-Curtis dissimilarities among the sampling sites using the R package  
228 BiodiversityR (Kindt 2017). We plotted the pairwise dissimilarities for each trait group as boxplots for visual  
229 inspection.

230

231 Second, to identify significant variables ( $\alpha = 0.05$ , 1000 permutations) structuring deconstructed assemblages  
232 within each biological trait group (see above), we conducted redundancy analyses (RDA) with a conservative

233 forward selection method (Blanchet et al. 2008) for two different explanatory variable groups separately:  
234 environmental or spatial variables. In the RDA-analysis, we used Hellinger-transformed abundance data  
235 (Legendre and Gallagher 2001) of each deconstructed assemblage. Forward selection was carried out only if  
236 the global test including all explanatory variables of a variable group was significant. Forward selection was  
237 conducted with two stopping rules: (1)  $p > 0.05$  or (2) the adjusted  $R^2$  of the reduced model exceeded that of  
238 the global model. RDAs with variable selection were conducted using the `ordiR2step` function in the R  
239 package `vegan` (Oksanen et al. 2013). Finally, for each biological species trait group separately, we  
240 conducted variation partitioning in RDA between environmental and spatial predictors using the `varpart`  
241 function in the R package `vegan` (Oksanen et al. 2013). Adjusted coefficients of determination (Adj.  $R^2$ ) are  
242 reported for all RDAs and associated variation partitioning (Peres-Neto et al. 2006).

243

244 Third, we also examined covariations among species of the studied biological traits using non-parametric  
245 Mann-Whitney U test to compare, 1) if body sizes are different between non-flying and flying species, or 2)  
246 between the species with free and attached eggs. We also tested the tendency of non-flying and flying  
247 species to lay free eggs or attach their eggs to solid substrates using cross-tabulation and Pearson's chi-  
248 square test based on relative proportions (%) of species.

249

## 250 **Results**

### 251 Overall variation in deconstructed assemblages

252 Assemblage variation measured by Bray-Curtis dissimilarities differed among body size groups, although the  
253 differences were not very strong. Assemblage variation decreased from the group of small-sized to medium-  
254 sized and to large-sized macroinvertebrates (Fig. 2). Assemblage variation also differed between the  
255 dispersal and oviposition modes. Bray-Curtis dissimilarities were clearly higher for flying than for non-  
256 flying assemblages, as well as higher for assemblages with species laying their eggs freely than for the group  
257 of species attaching their eggs (Fig. 2).

258

259 Effects of environmental and spatial variables on the deconstructed assemblages

260 Unique spatial effects on assemblage structure decreased with increasing macroinvertebrate body size (Fig.  
261 3A, Table 3). Unique and spatially-structured (shared) effects of local environmental conditions accounted  
262 for a larger share of variation in the assemblage structure of medium-sized and large-sized species than that  
263 of small-sized macroinvertebrates. Unexplained variation was larger for small- and medium-sized than for  
264 large-sized species. Large and small spatial scale variables accounted for the variation in the assemblage  
265 structure of small-sized species (Fig. 3B), whereas the assemblage structure of medium-sized and large-sized  
266 macroinvertebrates were best associated with large to intermediate spatial scale variables. Significant  
267 environmental variables explaining variation in the assemblages deconstructed by biological traits are given  
268 in the Supplementary Material Tables S3-9.

269

270 Spatial variables accounted for an equal unique proportion of variation in assemblage structure of flying and  
271 non-flying species (Fig. 4A, Table 3). Unique environmental and spatially-structured environmental  
272 variation accounted for a larger proportion of variation in the assemblage structure of non-flying than that of  
273 flying species. The contribution of unexplained variation was larger for flying than for non-flying  
274 assemblages. Spatial variation in the assemblage structure of flying species was mostly associated with large-  
275 scale spatial variables (Fig. 4B). On the other hand, the corresponding model of non-flying taxa included  
276 variables related to large, intermediate and small spatial scales.

277

278 Spatial variables uniquely accounted for an equal proportion of variation in the assemblage structure of the  
279 species laying their eggs freely to the water and that in the assemblage structure of the species attaching their  
280 eggs to various substrates (Fig. 5A, Table 3). The contribution of unexplained variation was clearly larger for  
281 taxa laying their eggs freely to the water than for species attaching their eggs to substrates. Local  
282 environmental conditions explained a larger proportion of variation in the assemblage structure of the species  
283 with attached eggs than those with free oviposition. The spatial model of the species with free eggs was  
284 related to large spatial scale variables, whereas a corresponding model of species with attached eggs included  
285 variables related large and intermediate spatial scales (Fig. 5B).

286

287 We found moderate covariation between the studied biological traits. Non-flying species were on average  
288 slightly larger than flying ones (Fig. S1a), although this difference was not statistically significant (Mann-  
289 Whitney test,  $U = 718$ ,  $P = 0.126$ ). The species attaching their eggs tended to be larger than those with free  
290 eggs (Fig. S1b) (Mann-Whitney test,  $U = 1180$ ,  $P = 0.081$ ). Non-flying species had a stronger tendency to  
291 attach their eggs (85 % of species) compared to flying species (58 % of species, Table S10) ( $\chi^2 = 5.26$ ,  $df = 1$ ,  
292  $P = 0.022$ ).

293

## 294 **Discussion**

295 Relative roles of environmental conditions and regional processes affecting metacommunity structuring have  
296 been shown to vary depending on various factors, including niche breadth (Pandit et al. 2009; Székely and  
297 Langenheder 2014), biological traits (Cottenie 2005; De Bie et al. 2012), taxonomic group (Vilmi et al.  
298 2016), habitat type (Cottenie 2005), successional stage of the habitat (Allen et al. 2011) and spatial scale  
299 (Verleyen et al. 2009). We observed similarly to previous studies (De Bie et al. 2012; Heino 2013) that  
300 species traits are important in shaping the contributions of environmental conditions and spatial processes to  
301 metacommunity organisation. Our observations supported the importance of all studied traits, i.e. body size,  
302 dispersal mode and oviposition behaviour, for the processes affecting metacommunity organisation. Our  
303 results of the spatial and environmental effects on the structuring of assemblages with differing body sizes  
304 mainly supported the *a priori* expectations (Table 1). Interestingly, the unique contribution of spatial effects  
305 decreased with increasing macroinvertebrate body size in our study. This finding is in contrast with the  
306 previous observations at comparable within-system (Padiál et al. 2014) and among-lake (De Bie et al. 2012)  
307 levels that have indicated positive relationships between organisms' body size and contribution of spatial  
308 processes to metacommunity organisation. The above-mentioned studies have, however, included multiple  
309 taxonomic groups from microorganisms, such as bacteria and unicellular algae, to macroorganisms, such as  
310 macrophytes and fish, whereas we examined the effect of body size within one ecological group of  
311 organisms. Therefore, our results suggest that, within a single ecological group and at a rather small spatial  
312 scale, the importance of spatial processes may decrease with increasing body size, whereas environmental

313 filtering may be a more important process for medium-sized to large-sized compared to small-sized species.  
314 This pattern may also result from the domination of flying dispersers in our data, since dispersal capacity is  
315 observed to associate positively with body size (Jenkins et al. 2007). Observations on caddisflies also suggest  
316 that an increase in body size increases species dispersal ability across terrestrial landscapes (Hoffsten 2004).  
317 Therefore, large-sized flying species may be effective dispersers and less prone to wind effects in often  
318 windy conditions of large lakes when compared to weaker flying small species. This may enable more  
319 effective habitat selection by large-sized species and, therefore, a stronger effect of local environmental  
320 conditions on large-sized than on small-sized species assemblages. We also observed higher amounts of  
321 unexplained and total community variation in small-sized assemblages than in large-sized assemblages,  
322 which may relate to an increase of wind and water current effects with decreasing body size of species (see  
323 Compton 2002; Schernewski et al. 2005; Rundle et al. 2007). In addition to these contrasting body size  
324 effects on metacommunity organisation in our present and some earlier studies (De Bie 2012; Padial et al.  
325 2014), Algarte et al. (2014) did not observe any consistent effects of cell size on the contributions of local  
326 environment and spatial processes to the structuring of periphyton assemblages.

327

328 Previous among-lake studies have suggested that dispersal mode may be one of the key factors determining  
329 lake metacommunity organisation (De Bie et al. 2012; Heino 2013). At the level of a single lake, we  
330 observed equal spatial and stronger environmental effects on the assemblage structure of non-flying  
331 compared to flying taxa. These results contrasted with our preliminary expectations (Table 1) and the results  
332 of previous studies (De Bie et al. 2012; Heino 2013). This may be due to a difference in habitat connectivity  
333 between studies with contrasting spatial settings (earlier among-lake studies versus our within-lake study).  
334 Contradictory results of meta-analyses have also indicated either high (Cottenie 2005) or minor (Soininen  
335 2014; 2016) importance of dispersal mode in determining the contributions of environmental and spatial  
336 processes to metacommunity organisation. We also observed higher amounts of assemblage variability and  
337 unexplained variation in the assemblages of flying species compared to those of non-flying taxa. We can  
338 only speculate whether this higher “random” or unexplained variation in flying species’ assemblages could  
339 result from the wind influence on their aerial dispersal stages. Alternatively, stronger effects of  
340 environmental filtering on the assemblage structure of non-flying compared to flying species may be due to

341 biological trait covariation, since a larger proportion of non-flying species attached their eggs compared to  
342 flying species (Table S10). Therefore, the stronger environmental filtering effect on the assemblages of non-  
343 flying species compared to the assemblages of flying species may also relate to the differences in the  
344 oviposition behaviour between these dispersal modes. This is because oviposition behaviour was the  
345 biological trait with the largest observed differences in the contributions of local environmental conditions to  
346 metacommunity structuring (Fig. 5).

347  
348 Although very rarely examined, we assumed that oviposition behaviour may be an important biological trait  
349 that affects invertebrate metacommunity organisation, i.e. the contributions of environmental filtering, spatial  
350 processes and stochasticity to variation in assemblage structure (see also Heino and Peckarsky 2014). We  
351 expected that the species attaching their eggs are more effective in selecting suitable living conditions for  
352 their offspring, and therefore, deconstructed assemblages of these species were expected to be mainly  
353 controlled by local environmental conditions. On the other hand, larger contributions of stochasticity were  
354 expected for the assemblage structure of species laying their eggs freely on the water surface. For example,  
355 the slowly-sinking *Chironomus* egg masses that are laid freely to the lake pelagic zone have been observed to  
356 distribute and drift even as fast as 20 km h<sup>-1</sup> along with the surface water currents (Davies 1976). As  
357 expected, we observed that local environmental conditions were more important in explaining variation in  
358 the assemblage structure of the species with attached eggs than that of the species laying their eggs freely on  
359 the water surface. On the other hand, spatial variables explained equal proportions of variation in the  
360 assemblage structure of the species with free and attached eggs. In addition, the amount of unexplained  
361 variation was clearly larger for species laying their eggs freely than for species attaching their eggs. This  
362 may indicate a higher importance of stochastic events in the metacommunity dynamics of the species laying  
363 their eggs freely to the water. Water currents have been observed to influence the spatial and temporal  
364 distribution of planktonic organisms (Ji et al. 2002; Schernewski et al. 2005). Eggs laid freely on the water  
365 surface may drift with water currents (Davies 1976; Pinder 1995) and are, therefore, prone to wind-driven  
366 changes in water currents (Huttula et al. 1996; Ji et al. 2002; Schernewski et al. 2005; Wu et al. 2016).  
367 Hence, a larger proportion of unexplained variation in the assemblage structuring of species with free eggs

368 than in the assemblages of species with attached eggs may be related to unmeasured effects of water  
369 currents.

370

371 We observed higher variability in the assemblage composition of small-sized and flying species, and of those  
372 species laying their eggs freely to the water surface. On the contrary, smaller assemblage variation was  
373 observed in the groups of species with large-size, without flying stages and attaching their eggs on the solid  
374 substrates. Interestingly, the amount of explained variation was regularly higher for assemblages with  
375 smaller assemblage dissimilarity (large-sized, non-flying and ‘attaching’ egg-laying behaviour) than for  
376 assemblages with larger among-site variation in species composition (small-sized, flying and free oviposition  
377 behaviour). We propose that one factor that may be related to the amount of unexplained variation in the  
378 species composition of our deconstructed assemblages could be wind, which is also a key factor explaining  
379 variation in direction water currents in large lakes prone to wind effects (Huttula et al. [1996](#); Ji et al. [2002](#);  
380 Qin et al. [2007](#)). Moreover, we propose that the species with small size, those with a flying adult stage and  
381 laying their eggs freely on the water surface are more prone to the combined effects of wind and surface  
382 water currents than large-sized, non-flying and species with attached eggs (see also Davies [1976](#)). We also  
383 suggest that, in the windy pelagic zones of large lakes, small-sized flying species may become subject to  
384 unintentional dispersing effects caused by wind more easily than large-sized species that are generally  
385 stronger fliers (Compton [2002](#); Hoffsten [2004](#); Rundle et al. [2007](#))

386

387 We observed that within-lake assemblage dissimilarity varied among trait groups, and this dissimilarity was  
388 related to the relative proportions of explained and unexplained variation in assemblage composition.  
389 Generally, less variation was explained in more dissimilar assemblages (small-sized, flying and species  
390 laying their eggs freely), whereas more variation was explained in more similar assemblages (large-sized,  
391 non-flying and species with attached eggs). We suggest that wind and related water currents may possibly  
392 relate to these patterns observed, whereas small-sized, flying and species with free eggs could be expected to  
393 be more prone to wind-water current effects than large-sized, non-flying and species attaching their eggs.  
394 Our results suggest that spatial processes may be important although generally less important than  
395 environmental filtering in structuring macroinvertebrate assemblages at within-lake levels. Interestingly,

396 among the studied biological traits, we observed the strongest effect of oviposition behaviour on the  
397 contribution of environmental filtering to metacommunity organisation. We also observed significant  
398 covariation between dispersal and oviposition modes, i.e. non-flying species tended to attach their eggs  
399 rather than to lay their eggs freely. Instead, these two modes of oviposition behaviour were nearly equally  
400 common among flying species. In addition, non-flying species and the species attaching their eggs tended to  
401 be larger than flying species and those laying free eggs. Therefore, these results imply that covariations  
402 among biological traits may affect the organisation of lake macroinvertebrate metacommunities.

403

404 In contrast to some previous studies (De Bie et al. 2012; Padial et al. 2014), we found that the effect of  
405 environmental filtering on metacommunity organisation increased and that of spatial processes decreased  
406 with increasing body size. These results suggest that the observed body size effects on metacommunity  
407 organisation between previous among-lake studies and our present study conducted within a single large lake  
408 may differ due to differences in habitat connectivity and body size ranges studied. First, the levels of  
409 connectivity between this study and previous among-lake studies are clearly different. Despite the relatively  
410 high connectivity between habitat patches in a single large lake, dispersal rates may vary with invertebrate  
411 body size. In our highly-connected study system, environmental filtering may be the most important  
412 structuring force for the large species capable of actively searching for and selecting favourable habitats. On  
413 the other hand, small-sized species may be more exposed to stochastic events, and be affected by the  
414 changing directions of winds and water currents (Ji et al. 2002; Qin et al. 2007). Second, our study focused  
415 only on a single ecological group, i.e. benthic macroinvertebrates, with moderate variability in body size,  
416 whereas previous studies have included multiple biological groups from microorganisms to vertebrates (De  
417 Bie 2012; Padial et al. 2014). Thus, keeping in mind the difference in body size range studied between our  
418 and the previous studies, our results make perfect sense for macroinvertebrate metacommunity organisation  
419 in highly-connected systems.

420

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425

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**Table 1** Expected and observed relative effects of spatial processes and environmental filtering on the structuring of deconstructed species groups (based on biological traits) with the shares of unexplained variation. NE = No expectations

	<i>Expectations</i>			<i>Observed</i>		
	Spatial processes	Environmental filtering	Unexplained	Spatial processes	Environmental filtering	Unexplained
<i>Body size</i>						
Small-sized	Larger	Smaller	NE	Larger	Smaller	Larger
Medium-sized	Intermediate	Intermediate	NE	Intermediate	Intermediate	Larger
Large-sized	Smaller	Larger	NE	Smaller	Larger	Smaller
<i>Dispersal mode</i>						
Flying species	Smaller	Larger	NE	Equal	Smaller	Larger
Non-flying species	Larger	Smaller	NE	Equal	Larger	Smaller
<i>Oviposition behaviour</i>						
Free eggs	NE	Smaller	Larger	Equal	Smaller	Larger
Attached eggs	NE	Larger	Smaller	Equal	Larger	Smaller

**Table 2** Mean, minimum and maximum values of the 17 environmental variables used as environmental predictor variables in the statistical analyses

Variable	Mean	Min.	Max.
Conductivity ( $\mu\text{S cm}^{-1}$ )	41.9	20.6	63.9
Oxygen concentration ( $\text{mg l}^{-1}$ )	9.5	6.9	10.7
$\text{NH}_4\text{-N}$ ( $\mu\text{g l}^{-1}$ )	4.0	2.5	17
$\text{NO}_2\text{+NO}_3\text{-N}$ ( $\mu\text{g l}^{-1}$ )	2.1	1.0	28
Total phosphorus ( $\mu\text{g l}^{-1}$ )	12.2	5	75
Al ( $\mu\text{g l}^{-1}$ )	31.0	5	306
Na ( $\text{mg l}^{-1}$ )	1.2	1.0	1.5
Si ( $\text{mg l}^{-1}$ )	2.0	1.4	2.5
Zn ( $\mu\text{g l}^{-1}$ )	6.0	5	32.1
Wind fetch (m)	853	142	2257
Slope (%)	6.0	0.5	16.8
Substratum mean particle size (mm)	155	16	401
Substratum diversity (Shannon H)	1.3	0.9	1.7
Epilithic algal biomass (Chl- <i>a</i> $\mu\text{g cm}^{-2}$ )	1.4	0.5	2.4
Organic substratum coverage (%)	3	0	47
Macrophyte coverage (%)	14	0	65
Fish biomass ( $\text{g } 100 \text{ m}^{-2}$ )	86	0	434

**Table 3** Unique and shared proportions of variations explained by local environmental variables and spatial variables in the structure of assemblages deconstructed by biological traits: body size (small-, medium- and large-sized), dispersal mode (flying and non-flying) and oviposition mode (freely laid eggs and attached eggs)

	Proportions of variations explained (Adj. R <sup>2</sup> )			
	Local environment unique	Shared	Spatial unique	Unexplained
Body size				
<i>Small-sized</i>	0.07	0.06	0.05	0.82
<i>Medium-sized</i>	0.12	0.02	0.04	0.82
<i>Large-sized</i>	0.10	0.14	0.02	0.74
Dispersal mode				
<i>Non-flying</i>	0.12	0.09	0.04	0.75
<i>Flying</i>	0.09	0.06	0.04	0.81
Oviposition mode				
<i>Free eggs</i>	0.06	0.06	0.03	0.85
<i>Attached eggs</i>	0.13	0.09	0.03	0.75



## Figure legends:

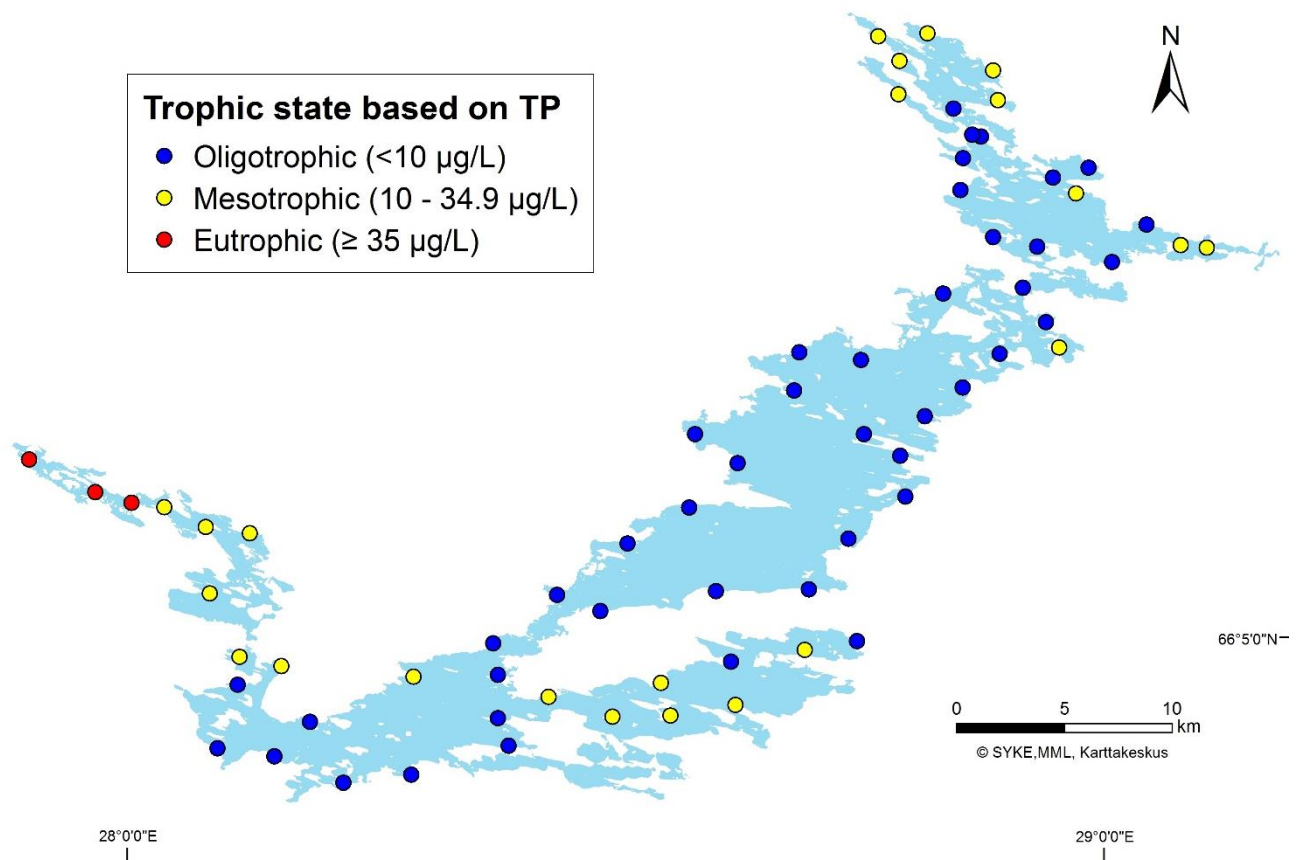
**Fig. 1** Map of Lake Kitkajärvi (Tolonen et al. 2017), where total phosphorus (TP) concentrations ( $\mu\text{g L}^{-1}$ ) are indicated by differently coloured symbols according to the OECD trophic state classification (OECD 1982). Shown are the 70 study sites

**Fig. 2** Among-site pairwise dissimilarity of the assemblages deconstructed by biological trait groups. The assemblage dissimilarities were measured using Bray-Curtis coefficient

**Fig. 3** Variation in the assemblage structure of littoral macroinvertebrate species in different body size categories (small, medium and large), partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between these two variable sets. They are shown **a** in adjusted coefficients of variation (adj.  $R^2$ ). **b** Ranks (V1-V27) and mean rank (bar) of the significant spatial variables in the RDA-models of small-sized, medium-sized and large-sized species

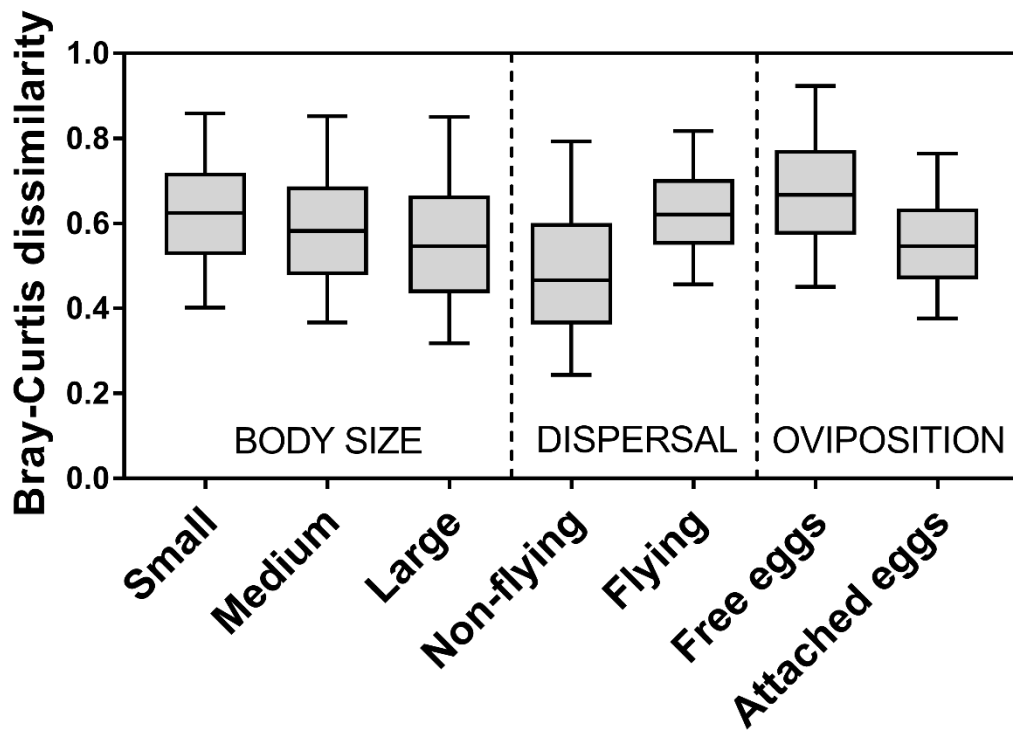
**Fig. 4** Variation in the assemblage structure of non-flying and flying littoral macroinvertebrate species partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between these two variable sets. They are shown **a** in adjusted coefficients of variation (adj.  $R^2$ ). **b** Ranks (V1-V27) and mean rank (bar) of the significant spatial variables in the RDA-models of non-flying and flying species

**Fig. 5** Variation in the assemblage structure of littoral macroinvertebrate species laying their eggs freely to the water (free eggs) or attaching their eggs to the substrates partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between these two variable sets. They are shown **a** in adjusted coefficients of variation (adj.  $R^2$ ). **b** Ranks (V1-V27) and mean rank (bar) of the significant spatial variables in the RDA-models of the species with free and attached eggs

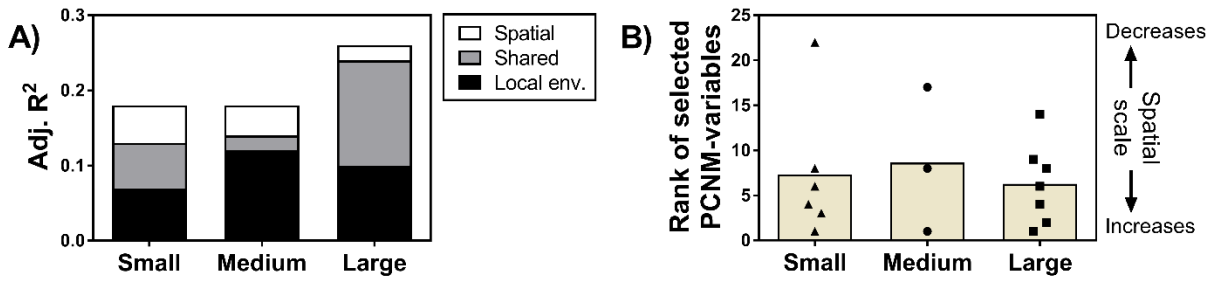


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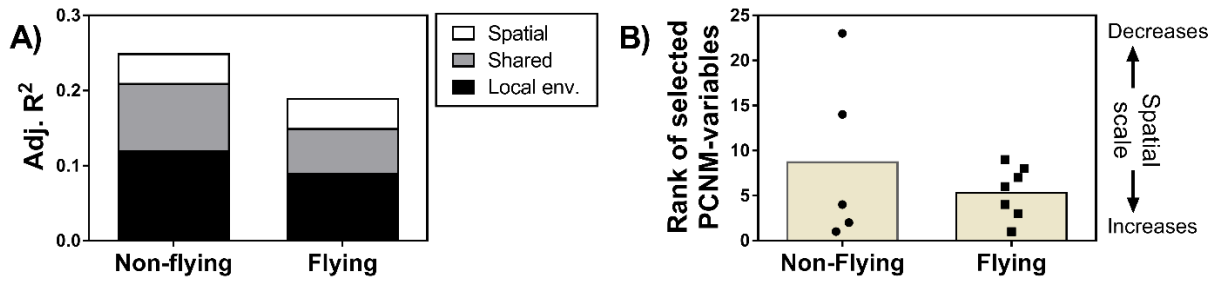
Shown are the 70 study sites



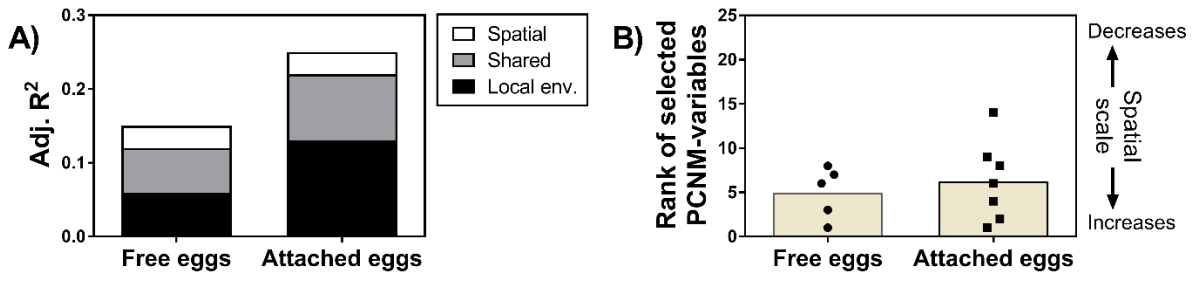
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**Fig. 3** Variation in the assemblage structure of littoral macroinvertebrate species in different body size categories (small, medium and large), partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between these two variable sets. They are shown **a** in adjusted coefficients of variation (adj. R<sup>2</sup>). **b** Ranks (V1-V27) and mean rank (bar) of the significant spatial variables in the RDA-models of small-sized, medium-sized and large-sized species



**Fig. 4** Variation in the assemblage structure of non-flying and flying littoral macroinvertebrate species partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between these two variable sets. They are shown **a** in adjusted coefficients of variation (adj. R<sup>2</sup>). **b** Ranks (V1-V27) and mean rank (bar) of the significant spatial variables in the RDA-models of non-flying and flying species



**Fig. 5** Variation in the assemblage structure of littoral macroinvertebrate species laying their eggs freely to the water (free eggs) or attaching their eggs to the substrates partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between these two variable sets. They are shown **a** in adjusted coefficients of variation (adj. R<sup>2</sup>). **b** Ranks (V1-V27) and mean rank (bar) of the significant spatial variables in the RDA-models of the species with free and attached eggs