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

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Abstract

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

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

Abstract

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Introduction

According to the metacommunity perspective, local communities are structured by the interplay between local environmental conditions and regional processes (Leibold et al. 2004), such as the intensity of dispersal between habitat patches and possible barriers for dispersal (Logue et al. 2011; Heino et al. 2015). Recently, metacommunity theory has become the dominant framework through which ecologists examine the structuring of biological communities (Brown et al. 2017). The four major paradigms of metacommunity ecology, i.e. species sorting through the process of environmental filtering (Leibold 1998), mass effects (Mouquet and Loreau 2002; 2003), neutrality (Hubbell 2001) and patch dynamics (Tilman 1994), are examples emphasizing some of the controlling factors of metacommunity dynamics (Logue et al. 2011; Brown et al. 2017). However, these paradigms fail to recognize the continuous and multidimensional nature of metacommunity dynamics (Brown et al. 2017). More recent views of metacommunity dynamics recognize, however, that dispersal and environmental filtering are not mutually exclusive (Gravel et al. 2006; Logue et al. 2011), and emphasize that dispersal and local environmental conditions simultaneously affect the structure of local communities. For example, adequate amount of dispersal is needed to enable species sorting through environmental filtering, whereas low dispersal rates result in increased effect of dispersal limitation on community assembly and high dispersal rates to the dominance of mass effects (Winegardner et al. 2012; Heino et al. 2015; Brown et al. 2017).

Biological traits are characteristics that relate to the environmental responses, dispersal and competitive abilities of species (McGill et al. 2006). Therefore, biological traits are keys to understand metapopulation and metacommunity dynamics, i.e. the responses of individual species and entire biotic communities to spatial processes and local environmental conditions (De Bie et al. 2012; Heino 2013). A suitable model group for examining trait-environment relationships by community deconstruction are littoral macroinvertebrates. This is because littoral macroinvertebrates show a diverse suite of biological traits related to feeding mode, substrate attachment, oviposition behaviour, body size, dispersal mode and dispersal abilities (Hanna 1961; Pinder 1995; Tolonen et al. 2003; Heino 2008; Heino and Tolonen 2017; Tolonen et al. 2017). For example, body size has been recognized as one of the key traits that may determine metacommunity structure because it is expected to be related to dispersal ability (De Bie et al. 2012). Generally, in larger spatial scale and among-lake studies, the effect of spatial processes in structuring communities increases and effect of local environmental conditions decreases with increasing body size of organisms (De Bie et al. 2012; Soininen 2016). However, these expectations of metacommunity structuring-species traits relationships may be different in highly-connected systems, such as a single large lake, and within a single ecological group, such as littoral macroinvertebrates. The dispersal mode of organisms has a key role in determining how species are spatially distributed and how they are interacting with their environment (Cottenie 2005). Passive dispersers (e.g. worms, clams and mussels) are dispersed by water currents or by larger animals (Bilton et al. 2001; Vanschoenwinkel et al. 2008), and they may have limited ability to actively select their habitats (Vanschoenwinkel et al. 2008). Active dispersers (e.g. flying insects) can actively select their habitats and oviposition sites to ensure favourable environmental condition for their offspring (Berendonk 1999; Resetarits 2001). Aerial dispersal is generally the most important mode of dispersal among lake littoral macroinvertebrates, and often the majority of species and individuals in macroinvertebrate communities consist of aquatic insects with flying adults (e.g. 56-61 % of abundance in Tolonen et al. 2001; Tolonen and Hämäläinen 2010). In addition to dispersal modes, divergent oviposition behaviours of freshwater macroinvertebrate species constitute important life history strategies (Verberk et al. 2008) that may also be related to community assembly (Heino and Peckarsky 2014). Many macroinvertebrate species attach their eggs selectively on solid substrates, such as on aquatic plants or on stones below water surface. Another common oviposition strategy is to lay eggs freely on water surface (Hanna 1961; Pinder 1995). Therefore, water currents within a lake may have important effects on the dispersal of some aquatic insect taxa (e.g. non-biting midges) due to the planktonic behaviour of their eggs (laid freely to the water surface) and first instar larvae (Davies 1976; Pinder 1995).

In this study, we examined the effects of local environmental conditions and spatial processes on the metacommunity organisation of littoral macroinvertebrates in a large lake system through deconstructing entire assemblages by biological trait groups. These traits included: (1) body size (small-, medium-, and large-sized), (2) dispersal mode (non-flying and flying), and (3) oviposition behaviour (free oviposition on water surface and selective oviposition on solid surfaces). Earlier across-taxonomic group, among-lake (De Bie et al. 2012) and larger spatial-scale studies (Soininen 2014; 2016) have indicated that spatial effects increase and environmental effects decrease with increasing body size of species in biotic assemblages. Opposite to these studies, we expected that, with increasing macroinvertebrate body size, the importance of environmental filtering increases and spatial processes decreases within a single lake system (Table 1). This is because the dispersal capacity of active dispersers has been observed to be positively correlated with body size (Jenkins et al. 2007) and, among flying aquatic insects, large species are generally stronger flyers than small ones (Compton 2002; Hoffsten 2004). Large-sized flying species are considered stronger dispersers and may be more able to move in an optimal (desired) direction in windy pelagic zones of large lakes (see Compton 2002; Rundle et al. 2007). Therefore, large species may be more effective in selecting oviposition sites and, hence, finding optimal habitats for their offspring when compared to small-sized species.

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

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

Material and methods

Sampling and identification of macroinvertebrates

In September 2013, littoral macroinvertebrates were sampled at 70 stony bottom sites, which covered all sub-basins and were located evenly around the entire perimeter of the Kitkajärvi lake system (surface area 305 km^2) in northeastern Finland (centered on 66º10‘N, 028º39‘E) (Fig. 1). Macroinvertebrates were sampled 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 for 30 s, were taken at 20 to 50 cm depth. This represented 6 m and 3 minutes sample size in total. When taking each of the 30 second subsample, the field worker moved backwards and simultaneously kicked the substrate, and moved the net from side-to-side close to the bottom. Samples were sieved using 0.5 mm mesh and preserved in ethanol in the field. In the laboratory, the samples were sorted and animals were counted and identified usually to species or genus, including the species-rich family Chironomidae. However, for the Oligochaeta, only a few common taxa were identified to species level. Water mites (Hydracarina) were not identified to lower taxonomic levels. All the work phases in field and laboratory were conducted by the same persons.

Measurements of local environmental variables

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

SFS), which are consistent with the pan-European standards (CEN, the European Committee for Standardization). Altogether 35 water chemistry variables were analysed from water samples taken at each sampling site (Supplementary Material Table S1).

Epilithic algal biomass (ELA BM) (chl-*a* µg cm^{-2}) was measured using *in vivo* fluorescence measurements by BenthoTorch portable benthic algae analyser (www.bbe-moldaenke.de/chlorophyll/benthotorch). Ten randomly selected stones were collected from the depth of 40 cm for BenthoTorch measurements at each site. Total surface area of the algal measurements was 9.6 cm^2. At each site, fish biomass was estimated by electrofishing without escape nets. Fish were sampled once from 100 m^2 area at each site (Sutela et al. 2016). Percentage (%) coverage of macrophytes was estimated from six 1 m × 1 m plots positioned randomly to the depths of 0-2 m along the transect perpendicular to the shoreline.

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

Spatial variables

Principal coordinates of neighbour matrix analysis (PCNM, Borcard and Legendre 2002) was conducted to produce spatial eigenvectors for the analyses of spatial structures in the littoral macroinvertebrate species composition. PCNM uses geographic (x and y) coordinates taking into account complex spatial structures, including those that are nonlinear and occur at multiple spatial scales (Borcard and Legendre 2002). PCNM analysis was conducted using the R package PCNM (Legendre et al. 2013). The analysis using coordinates of the 70 sampling sites resulted in 27 PCNM eigenvectors showing positive spatial autocorrelation. These eigenvectors were used as explanatory spatial variables in further analyses. First (V1, V2, V3, etc.) spatial variables represented large-scale and last (V27, V26, V25, etc.) small-scale spatial relationships among the sampling sites. Current nomenclature connects PCNM analysis to the framework of Moran's eigenvector maps, and PCNM eigenvectors are thus nowadays also called distance-based Moran's eigenvector maps (dbMEM) (Dray et al. 2012).

Classification of biological traits

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

Modelling variation in assemblage structure

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

Second, to identify significant variables ($\alpha = 0.05$, 1000 permutations) structuring deconstructed assemblages within each biological trait group (see above), we conducted redundancy analyses (RDA) with a conservative forward selection method (Blanchet et al. 2008) for two different explanatory variable groups separately: environmental or spatial variables. In the RDA-analysis, we used Hellinger-transformed abundance data (Legendre and Gallagher 2001) of each deconstructed assemblage. Forward selection was carried out only if the global test including all explanatory variables of a variable group was significant. Forward selection was conducted with two stopping rules: (1) $p > 0.05$ or (2) the adjusted R^2 of the reduced model exceeded that of the global model. RDAs with variable selection were conducted using the ordiR2step function in the R package vegan (Oksanen et al. 2013). Finally, for each biological species trait group separately, we conducted variation partitioning in RDA between environmental and spatial predictors using the varpart function in the R package vegan (Oksanen et al. 2013). Adjusted coefficients of determination (Adj. R^2) are reported for all RDAs and associated variation partitioning (Peres-Neto et al. 2006).

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

Results

Overall variation in deconstructed assemblages

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

Effects of environmental and spatial variables on the deconstructed assemblages

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

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

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

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

Discussion

Relative roles of environmental conditions and regional processes affecting metacommunity structuring have been shown to vary depending on various factors, including niche breadth (Pandit et al. 2009; Székely and Langenheder 2014), biological traits (Cottenie 2005; De Bie et al. 2012), taxonomic group (Vilmi et al. 2016), habitat type (Cottenie 2005), successional stage of the habitat (Allen et al. 2011) and spatial scale (Verleyen et al. 2009). We observed similarly to previous studies (De Bie et al. 2012; Heino 2013) that species traits are important in shaping the contributions of environmental conditions and spatial processes to metacommunity organisation. Our observations supported the importance of all studied traits, i.e. body size, dispersal mode and oviposition behaviour, for the processes affecting metacommunity organisation. Our results of the spatial and environmental effects on the structuring of assemblages with differing body sizes mainly supported the *a priori* expectations (Table 1). Interestingly, the unique contribution of spatial effects decreased with increasing macroinvertebrate body size in our study. This finding is in contrast with the previous observations at comparable within-system (Padial et al. 2014) and among-lake (De Bie et al. 2012) levels that have indicated positive relationships between organisms' body size and contribution of spatial processes to metacommunity organisation. The above-mentioned studies have, however, included multiple taxonomic groups from microorganisms, such as bacteria and unicellular algae, to macroorganisms, such as macrophytes and fish, whereas we examined the effect of body size within one ecological group of organisms. Therefore, our results suggest that, within a single ecological group and at a rather small spatial scale, the importance of spatial processes may decrease with increasing body size, whereas environmental filtering may be a more important process for medium-sized to large-sized compared to small-sized species. This pattern may also result from the domination of flying dispersers in our data, since dispersal capacity is observed to associate positively with body size (Jenkins et al. 2007). Observations on caddisflies also suggest that an increase in body size increases species dispersal ability across terrestrial landscapes (Hoffsten 2004). Therefore, large-sized flying species may be effective dispersers and less prone to wind effects in often windy conditions of large lakes when compared to weaker flying small species. This may enable more effective habitat selection by large-sized species and, therefore, a stronger effect of local environmental conditions on large-sized than on small-sized species assemblages. We also observed higher amounts of unexplained and total community variation in small-sized assemblages than in large-sized assemblages, which may relate to an increase of wind and water current effects with decreasing body size of species (see Compton 2002; Schernewski et al. 2005; Rundle et al. 2007). In addition to these contrasting body size effects on metacommunity organisation in our present and some earlier studies (De Bie 2012; Padial et al. 2014), Algarte et al. (2014) did not observe any consistent effects of cell size on the contributions of local environment and spatial processes to the structuring of periphyton assemblages.

Previous among-lake studies have suggested that dispersal mode may be one of the key factors determining lake metacommunity organisation (De Bie et al. 2012; Heino 2013). At the level of a single lake, we observed equal spatial and stronger environmental effects on the assemblage structure of non-flying compared to flying taxa. These results contrasted with our preliminary expectations (Table 1) and the results of previous studies (De Bie et al. 2012; Heino 2013). This may be due to a difference in habitat connectivity between studies with contrasting spatial settings (earlier among-lake studies versus our within-lake study). Contradictory results of meta-analyses have also indicated either high (Cottenie 2005) or minor (Soininen 2014; 2016) importance of dispersal mode in determining the contributions of environmental and spatial processes to metacommunity organisation. We also observed higher amounts of assemblage variability and unexplained variation in the assemblages of flying species compared to those of non-flying taxa. We can only speculate whether this higher “random” or unexplained variation in flying species’ assemblages could result from the wind influence on their aerial dispersal stages. Alternatively, stronger effects of environmental filtering on the assemblage structure of non-flying compared to flying species may be due to biological trait covariation, since a larger proportion of non-flying species attached their eggs compared to flying species (Table S10). Therefore, the stronger environmental filtering effect on the assemblages of non-flying species compared to the assemblages of flying species may also relate to the differences in the oviposition behaviour between these dispersal modes. This is because oviposition behaviour was the biological trait with the largest observed differences in the contributions of local environmental conditions to metacommunity structuring (Fig. 5).

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

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

We observed that within-lake assemblage dissimilarity varied among trait groups, and this dissimilarity was related to the relative proportions of explained and unexplained variation in assemblage composition. Generally, less variation was explained in more dissimilar assemblages (small-sized, flying and species laying their eggs freely), whereas more variation was explained in more similar assemblages (large-sized, non-flying and species with attached eggs). We suggest that wind and related water currents may possibly relate to these patterns observed, whereas small-sized, flying and species with free eggs could be expected to be more prone to wind-water current effects than large-sized, non-flying and species attaching their eggs. Our results suggest that spatial processes may be important although generally less important than environmental filtering in structuring macroinvertebrate assemblages at within-lake levels. Interestingly, among the studied biological traits, we observed the strongest effect of oviposition behaviour on the contribution of environmental filtering to metacommunity organisation. We also observed significant covariation between dispersal and oviposition modes, i.e. non-flying species tended to attach their eggs rather than to lay their eggs freely. Instead, these two modes of oviposition behaviour were nearly equally common among flying species. In addition, non-flying species and the species attaching their eggs tended to be larger than flying species and those laying free eggs. Therefore, these results imply that covariations among biological traits may affect the organisation of lake macroinvertebrate metacommunities.

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

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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

	Expectations			***Observed***		
	Spatial processes	Environmental filtering	Unexplained	Spatial processes	Environmental filtering	Unexplained
Body size						
Small-sized	Larger	Smaller	NE	Larger	Smaller	Larger
Medium-sized	Intermediate	Intermediate	NE	Intermediate	Intermediate	Larger
Large-sized	Smaller	Larger	NE	Smaller	Larger	Smaller
Dispersal mode						
Flying species	Smaller	Larger	NE	Equal	Smaller	Larger
Non-flying species	Larger	Smaller	NE	Equal	Larger	Smaller
Oviposition behaviour						
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 (µS cm^{-1})	41.9	20.6	63.9
Oxygen concentration (mg l^{-1})	9.5	6.9	10.7
NH_4-N (µg l^{-1})	4.0	2.5	17
NO_2+NO_3-N (µg l^{-1})	2.1	1.0	28
Total phosphorus (µg l^{-1})	12.2	5	75
Al (µg l^{-1})	31.0	5	306
Na (mg l^{-1})	1.2	1.0	1.5
Si (mg l^{-1})	2.0	1.4	2.5
Zn (µg 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-*a* µg cm^{-2})	1.4	0.5	2.4
Organic substratum coverage (%)	3	0	47
Macrophyte coverage (%)	14	0	65
Fish biomass (g 100 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^2)			
	Local environment unique	Shared	Spatial unique	Unexplained
Body size				
Small-sized	0.07	0.06	0.05	0.82
Medium-sized	0.12	0.02	0.04	0.82
Large-sized	0.10	0.14	0.02	0.74
Dispersal mode				
Non-flying	0.12	0.09	0.04	0.75
Flying	0.09	0.06	0.04	0.81
Oviposition mode				
Free eggs	0.06	0.06	0.03	0.85
Attached eggs	0.13	0.09	0.03	0.75

Figure legends:

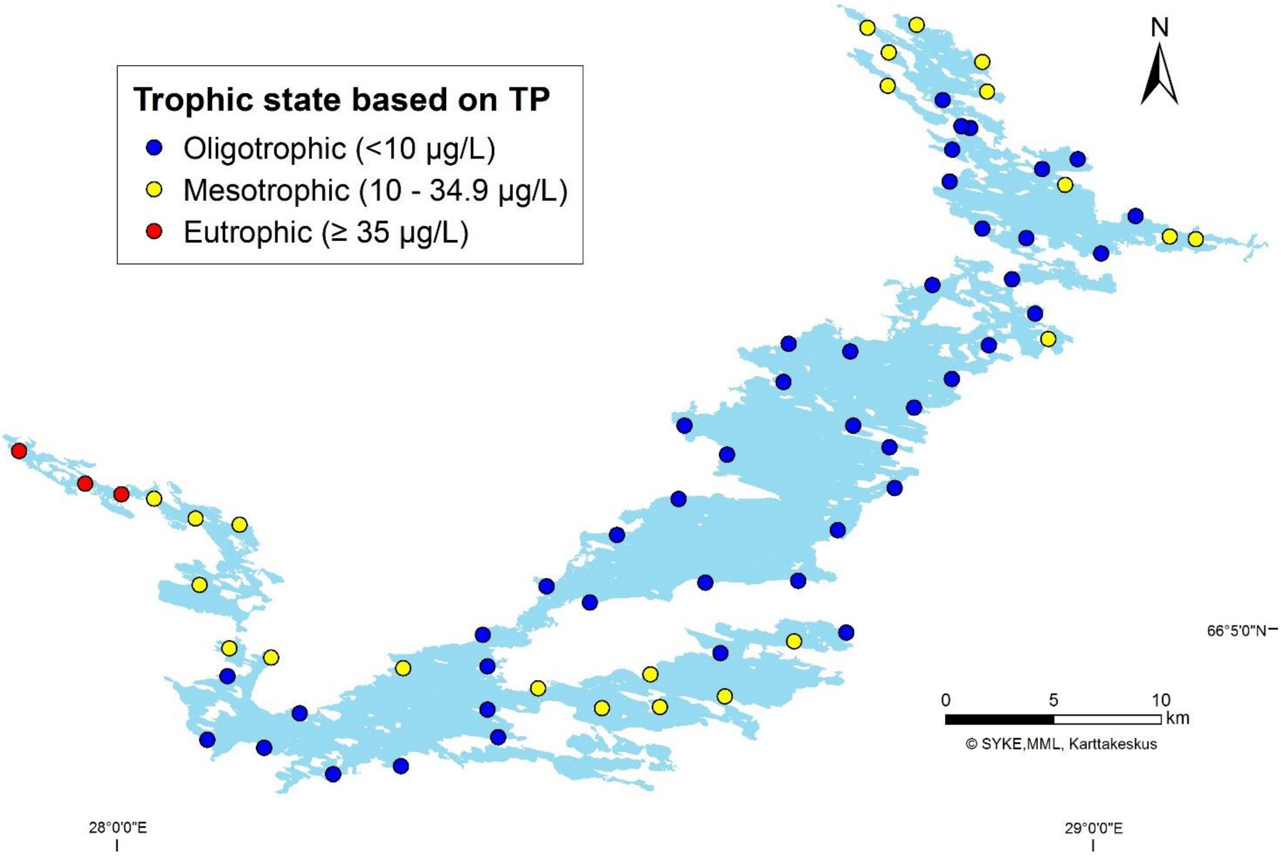
Fig. 1 Map of Lake Kitkajärvi (Tolonen et al. 2017), where total phosphorus (TP) concentrations (µg L^{-1}) are indicated by differently coloured symbols according to the OECD trophic state classification (OECD 1982). Shown are the 70 study sites

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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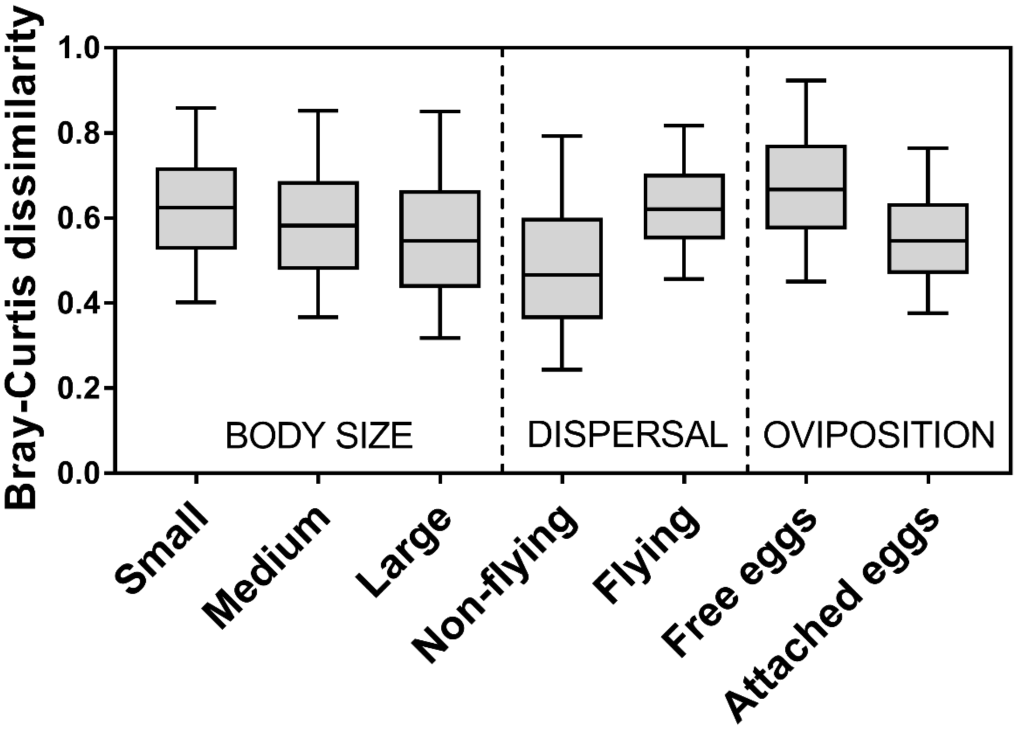
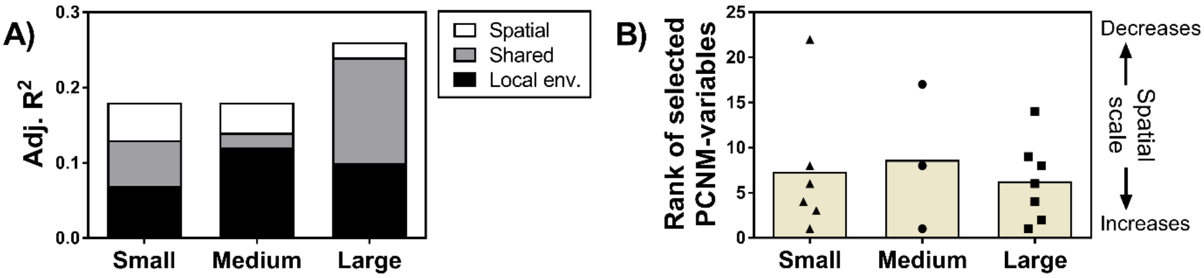


Fig. 2 Among-site pairwise dissimilarity of the assemblages deconstructed by biological trait groups. The assemblage dissimilarities were measured using Bray-Curtis coefficient



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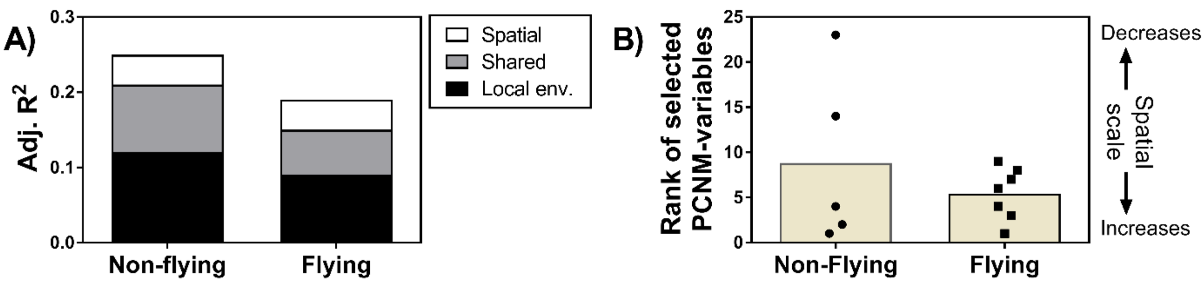

Fig. 4 Variation in the assemblage structure of non-flying and flying littoral macroinvertebrate species partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between these two variable sets. They are shown **a** in adjusted coefficients 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

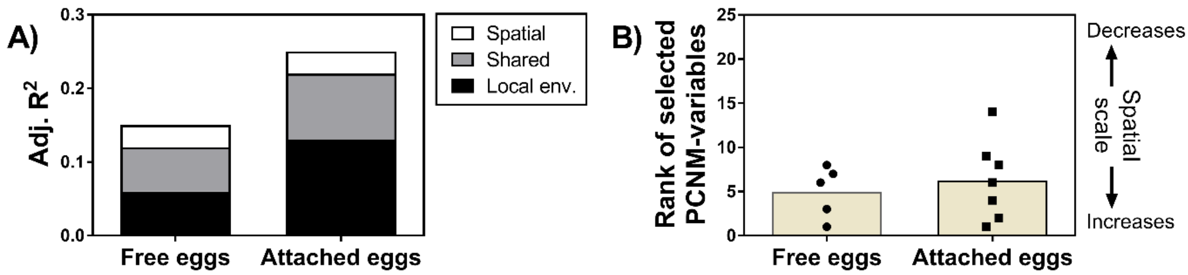

Fig. 5 Variation in the assemblage structure of littoral macroinvertebrate species laying their eggs freely to the water (free eggs) or attaching their eggs to the substrates partitioned to the fractions accounted for by local environmental variables, spatial variables and shared proportions between 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