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Environmental and spatial drivers of beta diversity components of chironomid metacommunities in contrasting freshwater systems

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Abstract Partition of beta diversity into components is a modern method that allows inferences about the underlying processes driving metacommunities. Based on two alternative approaches, we examined the patterns of beta diversity components of chironomids in relation to environmental and spatial gradients in three contrasting freshwater ecosystems. Beta diversity and its replacement component increased from environmentally less heterogeneous lake, through more complex wetland to stream network. Constrained ordination revealed that environmental heterogeneity and spatial processes explain some variation of the patterns of pairwise beta diversity components. Both beta diversity partitioning approaches emphasised the importance of habitat structure and food resource in structuring chironomid metacommunities. However, concurrent approaches provided contrasting results regarding the relative role of underlying mechanisms related to species replacement and richness. Therefore, further research is needed to clarify which of the beta diversity partitioning approaches should be preferred more widely in ecological studies.

Keywords dispersal, environmental filtering, assemblage, niche-based mechanisms, species richness, species turnover.

Introduction

Disentangling how and why assemblage composition changes from site to site is fundamental to understand many ecological processes, including principles of metacommunity organization and species coexistence (Leibold et al., 2004; Ricklefs, 2004). This issue is the main research frontier of beta diversity analyses, which received increased interest in the last decades, with many developments in theoretical and analytical grounds (e.g. Dray et al., 2006; Tuomisto, 2010a,b; Anderson et al., 2011; Logue et al., 2011).

It has been shown, for example, that pairwise beta diversity measures (i.e. which quantify the differences in the number and identity of species between two sites) can be decomposed into ecologically meaningful components. In fact, two concurring approaches have been elaborated recently to dissect components of differences in assemblages, which are related to the degree of differences in species richness or composition between sites. Baselga (2010, 2012; thereafter BAS approach) suggested that beta diversity could be dissected into a species turnover (also termed replacement) and a nestedness resultant component. *Sensu* BAS the turnover component accounts for the dissimilarity associated with the replacement of some species by others between assemblages and the nestedness resultant component accounts for the dissimilarity associated with species losses in which an assemblage is a strict subset of the other more species rich assemblage. Whereas, Podani & Schmera (2011; POD approach) proposed to decompose beta diversity into species replacement component *sensu* POD and richness difference component associated with species losses and gains irrespective of nestedness. The species turnover or replacement component in both approaches implies the simultaneous gain and loss of species due to environmental filtering, competition and historical events (Leprieur et al., 2011), and thus reflect the influence of ecological gradients on community structure (Legendre, 2014). Whereas, richness difference including its special case, the nestedness, may reflect diversity (number) of ecological niches available at different locations or other processes influencing the number of species (e.g. species introductions and physical barriers) (Legendre, 2014). BAS and POD approaches agree in that for practical purposes the relativized forms of these components should be used. However, it is important to note, that even the relativized species replacement components of the two approaches are calculated differently (although they have the same numerator, but are based on different denominators), and thus, these two measures are neither closely correlated to each other nor could represent the same ecological concept (Legendre, 2014; Baselga & Leprieur, 2015; Podani & Schmera, 2016). Soon after the introduction of pairwise diversity components, their multiple-site versions have also been established both for the BAS (Baselga, 2012) and POD (Ensing & Pither, 2015) approaches.

The relative importance of beta diversity components and related measures have been evaluated for several systems and it was concluded that their patterns could be highly variable across taxonomic groups and habitats as well as over time (e.g. Boieiro et al., 2013; Brendonck et al., 2015; Lewis et al., 2016; Alahuhta et al., 2017; Ruhí et al., 2017). Further, recent evaluation of experimental mesocosm data revealed that environmental heterogeneity and dispersal intensity could jointly affect the relative importance of species turnover (replacement) and nestedness resultant components *sensu* BAS in planktonic metacommunities (Gianuca et al., 2017). However, it is still less known how different environmental and spatial factors influence the relative importance of beta diversity components. Specifically, we do not exactly know whether there are specific environmental and spatial properties which could be more related to a particular component. Revealing the relationship of environmental and/or spatial gradients with these components can help us to better understand the drivers of beta diversity.

In this study we analyse how the relative importance of components of beta diversity could vary between metacommunities of different ecosystems and in relation to environmental and spatial gradients on the example of chironomids (Diptera: Chironomidae). Chironomids are abundant insects that occur in a wide-range of aquatic habitats and preferred model organisms of freshwater ecological studies. Thanks to their diverse and well-defined species specific environmental requirements chironomids have long been used as indicator organisms in both recent and paleolimnological studies (Brundin, 1958; Sæther, 1979; Gajewski et al., 2005; Milošević et al., 2013; Nicacio & Juen, 2015). Although adults may colonize new habitats rapidly, their flight is generally weak and dispersal happens predominantly passively by winds (Armitage, 1995). Accordingly, chironomid metacommunities are under conjunct control of environmental (i.e. niche-based environmental filtering) and spatial (i.e. dispersal limitation and mass effect) processes even at within lake and wetland scales (Árva et al., 2015a, 2017). However, so far there is only a sole study on the chironomids of spring fens (Rádková et al., 2014), which provides some insight into the small scale patterns of their beta diversity components using the POD approach.

Specific objectives of the study are: (a) to examine whether the patterns of beta diversity components (i.e. replacement and richness difference *sensu* POD and turnover (replacement) and nestedness resultant *sensu* BAS) of chironomid metacommunities contrast in different freshwater systems (i.e. a large and shallow lake, a wetland and a country-wide stream network); (b) to evaluate how these measures are related to between sites differences in various environmental properties (i.e. altitude, catchment, climate, landscape, and local physical-, chemical- and biotic habitat attributes) and spatial distribution of the local assemblages; and (c) to discuss agreement and differences between the results obtained by the two, commonly used, POD and BAS approaches.

Lake, wetland and stream network ecosystems are major freshwater habitat types, and in general, are under contrasting control of different spatial and environmental processes. Individual lakes generally show moderate environmental heterogeneity most of which concentrated in the littoral zone (Suurkuukka et al., 2012; Árva et al., 2015b) and involve no or little amount of within lake elements acting as dispersal constraints. Wetlands generally are mixtures of aquatic and terrestrial habitats, which exhibit high environmental heterogeneity. Due to their mosaic-like landscape pattern (Gibbs, 2000), dispersal capacity of certain aquatic taxa could be more limited in wetlands compared to lakes. Compared with lakes and wetlands, stream networks may represent the longest environmental gradients, often ranging through elevation and climatic zones. In addition, their dendritic topological structure may inherently restrict dispersal for many organisms (Erős & Campbell-Grant, 2015). Accordingly, for research point (a) we predicted that total beta diversity and its replacement (turnover) component will increase from lake, through wetland to stream network ecosystem due to differences in environmental heterogeneity and dispersal limitation effects between the three freshwater types. For research point (b) we predicted that contribution of relativized species replacement and richness related components to beta diversity will be influenced by both spatial and environmental factors, and the importance of spatial processes will increase along the supposed trend of dispersal limitation from lakes, through wetland to stream network. Finally, since BAS and POD approaches differ in their weighting between processes related to species replacements and richness (Carvalho et al., 2013; Baselga & Leprieur, 2015), for point (c) we predicted contrasting results on issues (a) and (b) depending on the approach followed.

Material and methods

Study area

We used three different freshwater systems for the purpose of this study. These included both lotic and lentic ecosystems, and they differed from each other considerably in their environmental characteristics, habitat complexity and spatial extent. The first is a large and shallow lake (Lake Balaton, Hungary), the second is a wetland (Kis-Balaton, Hungary), while the third is a country-wide stream network system (in Hungary; Fig. 1). Detailed descriptions of these large freshwater systems and maps showing the distribution of sampling sites are available in our recent papers (Árva et al., 2015a, 2017; Erős et al., 2017). Thus we present only a brief comparative description of the systems here.

Lake Balaton (46° 42' - 47° 04' N, 17° 15' - 18° 10' E; 104.8 a.s.l.) is a large (593 km^2) and shallow (mean depth: 3.2 m) lake. The lake is dominated by homogeneous open water habitat (>85% of the lake area), and consequently most of the environmental heterogeneity and biotic diversity are concentrated in the narrow littoral zone of ca. 200 m width only. Half of the shoreline is covered by reed grass stands, while its remaining part is strongly modified and covered by concrete buildings and ripraps. Small boat harbours situated within the reed grass stand and large sailing vessels and commercial ship harbours bordered by ripraps from waves occur along the whole shoreline and provide special habitats for the biota. In Lake Balaton, 128 sites distributed among the characteristic mesohabitats and across the lake area were sampled. Kis-Balaton (46° 34’ - 46° 42’ N, 17° 07’ - 17° 16’ E.; 106 m a.s.l.) is a very shallow (mean depth: <<1 m), lowland wetland area with a total extend of ca. 147 km^2. This wetland system is exceedingly heterogeneous with natural and semi-natural aquatic habitats, including large areas with open water, emergent, submerged and floating leaved aquatic macrovegetation, riparian vegetation, wet and inundated forests and meadows, canals either with and without currents, river habitats, ripraps, and separated borrow pits of variable succession stages, as well as extended patches of terrestrial vegetation. In Kis-Balaton, we sampled 79 sites representing the environmental heterogeneity of aquatic habitats and their distribution within the system. Whereas, the third study system, the stream network, included 51 running water (stream and river) sites, which distributed across the territory of Hungary (range of sites: 46^o 6' - 48^o 30' N, 16^o 12' - 22^o 50' E) in the Danube River catchment. Sampling sites were appointed to represent gradients in stream size (mean width: 1.6-186 m; mean depth: 0.015-3.0 m), altitude (from 85 to 261 m a.s.l.) and other influential environmental gradients in climate, landscape, current, substrate characteristics, macrophyte cover and chemical properties in the region.

Chironomid sampling

Benthic chironomid larvae were sampled between 26 June and 13 July 2012 in Lake Balaton and between 23 June and 01 July 2014 in Kis-Balaton. Sediment was sampled by means of Ekman grab and three merged cores taken within a 1 m^2 area represented the sample for each site. In addition, surface of stones from riprap habitats in equal area to the Ekman grab samples were cleaned and washed to plastic containers. Both sediment and stone periphyton samples were washed through a 0.25 mm mesh sieve and transported to the laboratory alive in a cooling box. Larvae were separated from sediment by sugar flotation method (Anderson, 1959), and then euthanized and stored in 70% ethanol until identification. Stream survey included two sampling occasions in August 2013 and March to April 2014. Chironomid assemblages were assessed according to the multi-habitat sampling protocol proposed by the AQEM project (AQEM Consortium, 2002; Hering et al., 2004). At each site 20 sample units were distributed along a 100 m long stream section to represent proportional area of mesohabitats present. Chironomids were “kick and sweep” sampled using a standard hand net (frame width: 25 cm; mesh size: 1 mm) by the same operator. Samples were preserved and stored in 70% ethanol for laboratory sorting and identification. Chironomid larvae were slide-mounted and identified to species or the lowest possible taxonomic levels.

Habitat assessment

Parallel to samplings, we measured series of environmental variables (see Appendix A in Electronic Supplementary Material) that have been found to influence assemblage structure of chironomids in the study region (Árva et al., 2015a,b, 2017; Schmera et al., 2018) and elsewhere (e.g. Real et al., 2000; Rae, 2004; Free et al., 2009; Puntí et al., 2009; Tóth et al., 2012). Considered aspects of regional and local environment included groups of variables related to altitude (in streams only), catchment size (in streams only), climate (in streams only), landscape, physical structure of sites, chemical properties of sites, and plants and their remains at sites. Since altitude, catchments size and climate were practically the same for all sites, these variables were not relevant in Lake Balaton and Kis-Balaton studies. Altitude was measured in the field with a GPS device (Garmin Montana 650). Catchment size data were obtained from database of the General Directorate of Water Management of Hungary. Climate variables included mean annual precipitation, number of sunny hours per year and mean annual air temperature data obtained from the CARPATCLIM Database © European Commission - JRC, 2013 (Szalai et al., 2013). Landscape variables for Lake Balaton were the lake basin (i.e. Keszthely-, Szigliget-, Szemes- and Siófok-basin; dummy coded), location along the north-to-south transect of the lake (i.e. northern littoral, offshore and southern littoral; dummy coded), and distances from the closest shore, reed grass stand, floating leaved or submerged macrophyte meadow and open water measured by a GPS device. In Kis-Balaton, landscape variables encompass distances from the closest clump, shore, reed grass stand, floating leaved or submerged macrophyte meadow, and open water. In addition, sites were classified as undisturbed and disturbed, with the latter indicating continuous or recent (i.e. within two years) habitat modifications (e.g. dredging, inundation, vegetation cutting). While, landscape variables for the country-wide stream survey included major land cover categories (CLC variables) obtained from the CORINE Land Cover 2006 (European Environmental Agency, 2010) and variables describing bank vegetation (see Appendix A in Electronic Supplementary Material).

Local physical, chemical and biotic (plants and organic matter) properties of sites were characterised in a very similar manner in Lake Balaton and Kis-Balaton. At each sampling site, we recorded water depth, Secchi disc depth, current (not relevant in Lake Balaton), temperature and redox potential (not measured in Kis-Balaton) of the uppermost sediment layer, and dissolved oxygen content, pH and conductivity of the water close to the bottom. Emergent, submerged, and floating leaved macrophytes, filamentous algae (*Cladophora* sp.), moss, riparian vegetation, and tree coverage (%) was estimated visually within a circle of 3 m diameter around the sampling point and the area of the submerged and floating leaved macrophyte stand was recorded by a GPS device and calculated by MapSource version 6.16.3. software (Garmin Ltd., www.garmin.com). The substratum of the sites was inspected for percentage compound of clay (grain size ≤0.002 mm), silt (0.002-0.06 mm), sand (0.06-2 mm), gravel (2-4 mm), rock (>200 mm), peat, mollusc shells and pure reed grass root (characteristic in some degrading reed grass stands of Lake Balaton). Occurrence of fine (FOM) and coarse (COM) decomposing organic matter particles, reed and tree leaves, and woody debris (excluding leaves) in the sediment, and occurrence of dead trees at the site was rated visually on a six category scale (0-5; where zero denotes absence and 1 to 5 correspond to the 1st to 5th 20% quantiles relative to the maximum observed abundance of that property in the area). Percentage organic matter content was assessed from dry (at 50^{o}C for 72-96 hours until constant mass was reached) samples of the upper most 2 cm sediment layer according to the loss-on-ignition method at 550^{o}C for 1 hour (LOI550; Heiri et al., 2001). In addition, chlorophyll-*a* was extracted from the upper 2 cm sediment layer by hot methanol method (Iwamura et al., 1970) in Lake Balaton, and from whole water column samples by acetone method (Aminot & Rey, 2000) in Kis-Balaton, and then, its concentration was measured spectrophotometrically (Shimadzu UV-1601 spectrophotometer).

In wadeable streams, 6-15 transects (depending on the complexity of the habitat; Sály et al., 2011) perpendicular to the channel were distributed along each 100 m long sampling section to measure wetted width, and water depth and current velocity (at 60% depth) at 3-6 (varied according to the channel width) equally spaced points. In non-wadeable streams and rivers, mean channel width was measured on Google Earth, while current velocity and water depth were averaged from 10-15 measurements along each sampling reach. All the other environmental variables were assessed in the same manner for all type of streams. The substratum of the sites was visually inspected for percentage compound of clay (grain size ≤0.006 mm), silt and sand (0.006-2 mm), gravel (2-60 mm), stone (60-400 mm) and rock (>400 mm), as well as for the relative amount of fine (FOM) and coarse (COM) decomposing organic matter particles. Note that these sediment components are not fully equivalent with those applied in lake and wetland systems. Water temperature, conductivity, dissolved oxygen content, and pH were measured with an OAKTON Waterproof PCD 650 portable meter, and concentration of nitrogen (i.e. nitrate and ammonium) and phosphorous (i.e. phosphate and total phosphorous) forms were assessed using Visocolor ECO field kits (Macherey-Nagel GmbH & Co. KG., Germany). Macro- and microalgae (i.e. diatoms; only when they formed visible patches, otherwise they received zero value), emergent, submerged and riparian macrophytes, tree coverage (%) were estimated visually for each sampling section.

Spatial variables

Distribution of sampling sites was modelled by sets of theoretical spatial variables using principal coordinate analysis of among site overland (in air-metres; aPCNM) and watercourse distances (in river-metres; wPCNM; for streams only) according to the modified method of

Borcard et al. (2004). The relative roles of overland and along watercourse dispersals are not yet fully explored in winged aquatic insects (e.g. Grönroos et al., 2013; Schmera et al., 2018; see also in Discussion), thus we calculated both overland and watercourse distances among the sites of the stream survey. Because these considerations have no or little relevance there, only "overland" geographical distances were used in Lake Balaton and Kis-Balaton. The PCNM variables model the position of each sampling site relative to all the other sites, similarly as they distribute on the map (Borcard et al., 2004; Dray et al., 2006). The procedure we followed to generate PCNM variables however differs in part from the original approach elaborated mainly to identify periodic distance related patterns in the nature (Borcard & Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). Specifically, we did not truncate the distance matrix, but rather used a logarithmic transformation of pairwise distances. The reason of this modification was that we wanted to use spatial variables to model distance and position related dispersal processes with an assumption that the probability of dispersal limitation increases with the geographical distance at a decreasing rate. We believe that logarithmic transformed distance data are more appropriate to capture patterns related to dispersal limitation than distance data truncated according to a subjective distance threshold (e.g. the largest distance between the closest neighbouring sites), and then applying an artificial multiplier for larger distances (e.g. four times the largest distance between the closest neighbouring sites) as originally proposed by Borcard & Legendre (2002). So we constructed matrixes of log(x+1) transformed Euclidean overland and watercourse (in streams only) distances between all pairs of sampling sites obtained from the GPS coordinates and the National GIS Database of Hungary (Institute of Geodesy, Cartography and Remote Sensing, Hungary), respectively, and subjected them to principal coordinate analyses using Past 2.17 software (Hammer et al., 2001) to obtain desired sets of PCNM variables. In order to limit the number of potential explanatory variables used in the statistical analysis, we used only the first 20 PCNM variables in each data set and excluded all the others with low eigenvalues (<1%), which presumably have little ecological relevance.

Calculation of beta diversity and its components

Here, we briefly summarise the basic algebra of the BAS and POD approaches following Legendre's (2014) system of symbols. We used the Jaccard index for measuring pairwise similarity (S_J) and 1-S_J for measuring beta diversity (i.e. Jaccard dissimilarity; D_J) among the sampling sites. Beta diversity was further decomposed into relativized additive fractions of species replacement ($Repl_{PJ}$) and richness difference ($Rich_{PJ}$) components according to the POD method (Eq. 1; Podani & Schmera, 2011), and species replacement ($Repl_{BJ}$) and nestedness-resultant (Nes_{BJ}) components according to the BAS method (Eq. 2; Baselga, 2012):

$$D_J = 1 - S_J = \frac{b+c}{a+b+c} = Repl_{PJ} + Rich_{PJ} = \frac{2\min(b,c)}{a+b+c} + \frac{|b-c|}{a+b+c} \quad (1)$$

$$D_J = 1 - S_J = \frac{b+c}{a+b+c} = Repl_{BJ} + Nes_{BJ} = \frac{2\min(b,c)}{a+2\min(b,c)} + \frac{a}{a+2\min(b,c)} * \frac{|b-c|}{a+b+c} \quad (2)$$

where a is the number of species present in both sites, whereas b and c represent the number of species present only in the first and second, respectively. Equations (1) and (2) can be re-arranged as:

$$1 = S_J + Repl_{PJ} + Rich_{PJ} \quad (3)$$

$$1 = S_J + Repl_{BJ} + Nes_{BJ} \quad (4)$$

respectively. These relationships summarize the relative amount of similarity (proportion of common species) and difference (beta diversity) related to species replacement and richness difference, and species replacement and nestedness-resultant between the species pools of two sites according to the POD (Eq. 3) and BAS (Eq. 4) approaches, respectively. If these relativized values are calculated for all pairs of sites, then one can analyse components of species level variations in a system including the 2D simplex graphical approach (Podani &

Schmera, 2011) and relate them to environmental and spatial patterns using constrained ordination and variation partitioning procedures.

Although pairwise indexes are good descriptors of between sites patterns across the studied system, but as it has been shown, they cannot account properly for co-occurrence patterns of species in many sites, and thus, may not be ideal tools for comparing whole systems (Diserud & Ødegaard, 2007; Baselga, 2013). Therefore, we also used multiple-site measure of Jaccard dissimilarity and its components to assess the amount of total beta diversity (multiple-D_J) and species replacement (multiple-$Repl_{PJ}$) and richness difference (multiple-$Rich_{PJ}$) according to the POD approach (Ensing & Pither, 2015), and species replacement (multiple-$Repl_{BJ}$) and nestedness-resultant (multiple-Nes_{BJ}) according to the BAS approach (Baselga, 2012).

Statistical analysis

In order to get more robust data for seasonal stream surveys with many single- and doubleton taxa in the samples, chironomid samples from the two sampling occasions were merged, whereas related environmental data were averaged by sites prior to analyses. Moreover, since pairwise beta diversity partitioning approaches cannot handle zero values, sampling sites without chironomids (zero sites in lake, three in wetland and one in stream network) were excluded from the analyses.

We used individual based rarefied (10,000 permutations) taxon richness curves produced with EcoSim 7.72 software (Gotelli & Entsminger, 2011) to compare total (gamma) diversities among the three study systems and to evaluate the adequacy of sampling effort in terms of detection of taxa (Gotelli & Colwell, 2001). To visualise the relationship between the species composition of the three ecosystems and the amount of among sites variation in their metacommunities, we performed non-metric multidimensional scaling (NMDS) analysis for sampling sites based on the Jaccard dissimilarity index with PAST 2.17 software (Hammer et al., 2001). In addition, among sites differences in environmental conditions were demonstrated by performing standardized principal component analysis (PCA) for each ecosystem also with PAST 2.17 software (Hammer et al., 2001). These latter results are presented in Appendix B (in Electronic Supplementary Material).

Total chironomid beta diversity was assessed by calculating multiple-D_J and its multiple-site components for lake, wetland and stream network ecosystems. Since multiple-site indices might be sensitive to differences in the number of sites sampled (Baselga 2010), we resampled 1000 times the lake and wetland data set to the sample size of stream network (n=50), and calculated the mean and the true 95% confidence interval (CI) of each measure for the resampled data sets. Analyses were performed in R (R Core Team, 2015) using the *betapart* package (Baselga et al., 2017). The R-script for this analysis is provided in the appendix in Ensing & Pither (2015).

Trends of pairwise beta diversity in the three study systems were first visually evaluated using 2D simplex graphical analysis (Podani & Schmera, 2011, 2016) according to the POD and BAS approaches based on equations (3) and (4), respectively. Then, pairwise index values were averaged across all pairs of sites to obtain an alternative percentage decomposition of total beta diversity into its components in each community (Podani & Schmera, 2011; Legendre, 2014). Note that the 2D simplex analysis of beta diversity components have been proposed specifically for the POD approach, and since species replacement and nestedness-resultant components *sensu* BAS has no meaningful complements, this analysis holds less analytical potential in the BAS approach (Podani & Schmera, 2016). However, to provide some comparative insight into the analytical capacity of the two concurring beta diversity partitioning approaches we show 2D simplex results for the BAS approach as well. Variability of pairwise site scores of each measure was inspected across study systems with permutational one-way analysis of variance (pANOVA; with 999 permutations) and permutational *t* post-hoc test performed in R (R Core Team, 2015) using the *anova.1way.R* and *t.perm.R* functions written by P. Legendre (available at: http://adn.biol.umontreal.ca/~numericalecology/Rcode/; accessed 05 February 2018). Differences between the two coherent pairwise beta diversity components was analysed in each metacommunities and separately for the POD and BAS approaches with permutational *t*-test.

To evaluate the role of different environmental and spatial (PCNM) variables in the variability of pairwise beta diversity components in the studied chironomid metacommunities, we performed partial direct gradient analysis followed by a variation partitioning approach (Cushman & McGarigal, 2002; Peres-Neto et al., 2006). We run the analyses based on both the POD and BAS approaches and using sites scores from equations (3) and (4) like in the 2D simplex analysis. We preferred this approach over analysing each beta diversity component individually (e.g. via multiple regression or distance based RDA models: Boieiro et al., 2013; Legendre, 2014; Baselga & Leprieur, 2015; Alahuhta et al., 2017) because relativized pairwise beta diversity components and similarity behave similarly, like percentage relative abundances of species. Since these measures sum up to one, their values are not independent from each other and consequently, it could be beneficial to evaluate them collectively. First, we calculated matrixes of between site Euclidean distances for each environmental and spatial variable. These pairwise differences in each specific environmental and spatial variable served then as potential explanatory variables in the multivariate analyses. Of explanatory variables, those measured on continuous scales and representing percentage distribution were log(x+1) and $\arcsin\sqrt{x}$ transformed, respectively. Categorical and dummy coded local environmental, pH and spatial PCNM variables were not transformed (see Appendix A in Electronic Supplementary Material). Since preliminary detrended correspondence analysis (DCA) indicated moderate gradient lengths in response variables (i.e. pairwise similarity and beta diversity components) for all three study systems and for both POD and BAS approaches (ranging between 1.63-1.90 and 1.84-2.08 in S.D. units, respectively), we chose redundancy analysis (RDA) for further evaluation (Lepš & Šmilauer, 2003). Potential explanatory variables were filtered for collinearity at $r>0.7$ and subjected to a forward stepwise selection procedure (at $P<0.05$) in RDA based on Monte Carlo randomization test with 9,999 unrestricted permutations. Then, to partition effects of significant variable groups (i.e. altitude, catchment, climate, landscape, physical site properties, chemical site properties, aquatic plants and decomposing organic matter, and spatial) on pairwise beta diversity components of local chironomid assemblages, a series of RDAs and partial RDAs were conducted (Cushman & McGarigal, 2002). DCAs and RDAs were performed using CANOCO version 4.5 software (ter Braak & Šmilauer, 2002).

Results

Gamma and alpha diversities

Sampling yielded a total of 13,804 individuals and a system level gamma diversity of 40 taxa (identified at species, species group and genus levels) in lake, 9,321 individuals and gamma diversity of 56 taxa in wetland, and 6,138 individuals and gamma diversity of 120 taxa in the stream network. The cumulative number of observed taxa for the three systems was 157. Proportions of both rare taxa (i.e. single- and doubletons) and taxa with limited distribution (presenting at one or few sites only) were substantial and varied considerably among systems (Appendix C in Electronic Supplementary Material). The number of rare taxa was highest in stream network (16 singletons and 12 doubletons, 13.3% and 10.0% of the total taxa, respectively), intermediate in wetland (nine singletons and two doubletons, 16.1% and 3.6%) and lowest in lake (four singletons and one doubleton, 10.0% and 2.5%). In stream network, 29 taxa presented at one site and 23 taxa at two sites only. The same values were 14 and seven in wetland, and five and three in lake. Taxon richness per site (alpha diversity) ranged between two and 22 (mean: 8.2; median: 8) taxa in lake, between zero and 25 (6.6; 6) taxa in wetland, and between zero and 35 (14.6; 14) taxa in stream network.

Individual based rarefaction analysis also approved highest chironomid gamma diversity in stream network, intermediate gamma diversity in wetland and lowest gamma diversity in lake (Fig. 2). Separation of 95% true CIs of rarefied species richness values among the three systems indicates that these differences are significant (at $P<0.05$). However, since neither of the rarefaction curves reached a trivial asymptote, it is very likely that more samplings would detect additional taxa in all three systems, especially in stream network.

Total beta diversity

Multiple-D_J indicated extremely high total chironomid beta diversity for the three systems (Table 1). In addition, although the 95% CIs of resampled multiple-D_J separated slightly between lake and wetland systems, differences between the mean multiple-D_J values of the three systems (multiple-D_J=0.969 in lake, 0.976 in wetland and 0.976 in stream network) could be assumed negligible from the practical point of view. More contrasting differences were found between the three systems in the decomposition of beta diversity into its components, especially based on the POD approach (Table 1). Multiple-$Repl_{PJ}$ proved to be highest (0.647) and multiple-$Rich_{PJ}$ lowest (0.328) in stream network, while 95% CIs of both measures overlapped between lakes (resampled means: 0.537 and 0.433, respectively) and wetlands (resampled means: 0.513 and 0.433, respectively). On the other hand, the BAS approach counted almost all of the total beta diversity (D_J) to be replacement related component with little or no differences in multiple-$Repl_{BJ}$ values between the three systems. NMDS plot shows that chironomid metacommunity of the stream network had clearly different species composition than metacommunities of the lake and wetland ecosystems (Fig.

3). This analysis somewhat oppugn the results of multiple-D_J and revealed that the lake chironomid metacommunity could be a nested subset of the wetland fauna with substantially lower internal variability.

Pairwise beta diversity

2D simplex analysis revealed medium to high mean pairwise beta diversity (i.e. low S_J, mean values ranging between 0.163 in wetland and 0.254 in lake; Table 2) in chironomid metacommunities according to the POD approach. Thus pairwise site scores tended to concentrate close to the left side of the ternary diagram, especially in wetland and stream network, but less markedly in lake (Fig. 4a-c). Replacement component of the pairwise beta diversity proved to be slightly more important than the richness difference component in lake and wetland chironomid communities, while in stream network mean replacement was about two times higher than mean richness difference. Mean $Repl_{PJ}$ trended as lake<wetland<stream network, while mean $Rich_{PJ}$ was highest in wetland and lowest in stream network.

2D simplex analysis under the BAS framework suggested that pairwise beta diversity was clearly dominated by the replacement component in all of the three systems with mean values following a trend of lake<wetland<stream network (Table 2; Fig. 4d-f). Mean $Nest_{BJ}$ proved to be similar in lake and wetland, while it was lowest in stream network.

Environmental and spatial patterns of pairwise beta diversity components

In general, the RDA models explained very similar amount of variance in pairwise beta diversity components of chironomids according to the POD and BAS approaches, although the importance of certain explanatory variables and their participation in the final models varied between the two approaches (Table 3; Fig. 5). Total explained variance was lowest in wetland (15.4% and 17.2% in the POD and BAS approaches, respectively), intermediate in lake (22.0% and 27.4%) and highest in stream network (25.2% and 24.9% in models with aPCNM, while 31.9% and 29.6% with wPCNM). Pure effect of spatial predictors was negligible (1.5%) in lake, while they explained 3.6-5.4% and 9.9-13.2% of variance in pairwise chironomid beta diversity components in wetland and in stream network, respectively. In stream network, wPCNMs proved to be more effective predictors than aPCNMs based either on their total or pure effect (Fig. 5). On the other hand, pure between site distances were filtered out from all models (i.e. study area × approach type) during the variable selection procedure.

Pairwise beta diversity components of chironomid assemblages were more related to environmental than to spatial predictors in all three systems and based on any approaches (Fig. 5). Further, spatial and environmental effects proved to be largely independent as their shared effect remained under 4% in all cases. In lake, environmental variables classified to site physical properties and plants and organic matter groups had the highest predictive power (Table 3). According to the POD approach, increase of richness difference component of beta diversity coincided with increases of between sites differences in distances from the shore, reed and submerged macrophyte stands and in water depth, while species replacement component increased with increasing between sites differences in physical substrate properties, dissolved oxygen concentration, LOI550 and macroalgae coverage (Fig. 6a). Similar tendencies were obtained based on the BAS approach for the nestedness resultant and species replacement components, respectively (Table 3; Fig. 6d). Likewise in wetland, variables belonging to site physical properties and plants and organic matter groups were the most effective predictors of pairwise beta diversity components of chironomids (Table 3). However, the total amount of variance captured by environmental variables was only moderate, especially in the POD approach, and no clear coincidence appeared on the ordination chart between the vectors of beta diversity components and explanatory variables, except between replacement component of the BAS and between sites differences in macroalgae coverage, presence of rock, water temperature and conductivity (Fig. 6b,e). In stream network, between sites differences in landscape, site physical, chemical, and plant and organic matter related properties proved to be more or less similarly effective predictors based on their pure effects (Table 3). In this system, increase of richness difference component of the POD approach coincided with increases of between sites differences in concentration of fine decomposing organic matter particles and mean annual air temperature, and decrease of difference in landscape coverage by artificial, non-agricultural vegetation (CLC14) (Fig. 6c). Replacement component of the POD proved to be most related to between sites differences in clay and stone components of the sediment, water current, dissolved oxygen content of the water and catchment area. Very similar environmental patterns were revealed for the nestedness resultant and replacement components of the BAS approach as well (Fig. 6f). Pairwise assemblage similarities correlated negatively with differences in influential environmental properties in all instances (i.e. the less their environments differed the more local assemblages were similar). However, pairwise similarities correlated positively with specific spatial predictors in some cases, specifically in stream network based on the BAS approach and less tightly in wetland based on the POD (Fig. 6).

Discussion

In this study we evaluated metacommunity patterns of chironomids in three different freshwater ecosystems utilizing the quantification tool of beta diversity components. As assumed, the three metacommunities differed largely in their species pools (gamma diversities) and taxa composition. The values of beta diversity, the relative contribution of particular beta diversity components and their relatedness to environmental and spatial variables also differed markedly. The results obtained from different analyses and based on concurring beta diversity partitioning approaches (i.e. BAS and POD) also contrasted in some respect.

We assumed that environmental heterogeneity increases from individual lake, through individual wetland to country-wide stream network (see Appendix B in Electronic Supplementary Material; site scores are most concentrated in lake and less in stream network ecosystem in PCA plot based on environmental variables), and accordingly, diversity of chironomid metacommunities should increase along the same trend. Although, total species richness (gamma diversity) followed this trend, results about the patterns of beta diversity were less consistent. For example, the multiple-site Jaccard dissimilarity index suggested very similar and extremely high total beta diversity for all three metacommunities, with index values close to their fundamental maximum of one. We consider this result however to be somewhat misleading, which may be related to the weakness of this measure in effectively comparing beta diversity of the samples. Specifically, an index value of one should indicate that all sites are inhabited by completely different composition of species (there are no common species at any two sites). However, this is clearly not the case in our study systems, since the lake metacommunity was represented by only 40 detected taxa for the 128 sites sampled and the wetland metacommunity by 56 taxa for 76 sites, which indicates that many species should be presented at more than one site even at the highest beta diversity possible under such conditions. Nevertheless, means of pairwise Jaccard dissimilarity also indicated high beta diversity for all three metacommunities, but with clear variability among the studied systems. As we hypothesised, mean pairwise beta diversity proved to be the lowest in lake. This system is dominated by open water habitat representing lower environmental heterogeneity compared to the more complex wetland and stream network systems. On the other hand, contrary to our hypothesis wetland metacommunity received higher mean pairwise beta diversity score than stream network metacommunity. We consider that this finding may reflect a methodological bias and be related to the higher environmental resolution of point samples in wetland compared to section level samples in streams.

We hypothesised that the relative role of the replacement component of beta diversity will increase from lake, through wetland to stream network ecosystem, because higher environmental heterogeneity is likely to favour more intense replacement (turnover) of species from site to site as a result of environmental filtering (species sorting). This assumption was clearly proved based on the pairwise replacement components of the POD and BAS approaches. Whereas, multiple-site replacement component measure (either based on the POD or BAS approach) provided similar scores for lake and wetland. Irrespective of the index type (i.e. multiple-site or pairwise) and the approach (i.e. POB or BAS) used, species replacement was the predominant component of beta diversity in all systems with most marked dominance in stream network. In stream network the high species richness relative to number of sites investigated (120 taxa for 50 sites) resulted more intense species replacement compared to wetland and especially lake ecosystems, which had substantially less species relative to the number of sites. A similar trend in the replacement component relative to species richness was observed in lichen communities by Nascimbene et al. (2013). For aquatic macrophytes, however, Alahuhta et al. (2017) also showed that variation in species composition (i.e. species replacement) primarily accounts for beta diversity in high-diversity regions, while in low-diversity regions richness difference related processes may have noticable role as well.

Richness difference component *sensu* POD and nestedness resultant *sensu* BAS contributed clearly the least to beta diversity in stream network. Since richness difference is mainly related to variability of number of ecological niches available across sites, it is not surprising that in stream network, where each sample covered wider range of habitats than individual point samples in lake and wetland, received lower scores for these beta diversity components. Therefore, variability of number of available niches across sites seemed to be more influential in organizing lake and wetland metacommunities of chironomids with slightly higher pairwise richness difference component scores in wetland. Since chironomids may occur in high diversity along wide ranges of ecological gradients, it is expectable that their metacommunities are more influenced by species replacement, than mechanism related to richness difference (Rádková et al., 2014). However, under extreme environmental conditions their species richness can be very low as well. Our lake and wetland areas included some sites with very low dissolved oxygen concentration and poor food supply, conditions which could be tolerated only by few species, and therefore, these sites could support richness difference related beta diversity. In accordance with our observations, environmental heterogeneity along with the size of the species pool (i.e. gamma diversity) were also identified as the main drivers of pairwise beta diversity components in chironomids at very small spatial scale in spring fens (Rádková et al., 2014). Results on chironomids from different freshwater systems thus also support the fact that regardless of the observed biota, environmental heterogeneity is likely the most important driver of beta diversity (Rosenzweig, 1995; Leibold et al., 2004; Heino et al., 2015).

In this study both the POD and BAS approaches supported the conclusion that the contribution of particular beta diversity components to total beta diversity varied substantially among the three systems. However, results obtained based on the two approaches are not in full agreement in that how chironomid beta diversity is organized. Namely, as it had been shown earlier, the BAS approach gives more weight to the species replacement component than the POD approach (Carvalho et al., 2013; Baselga & Leprieur, 2015) and this difference is apparent in this study as well (Table 1 and 2). Nevertheless, the predominant contribution of the replacement component in all three systems was consistently indicated by both approaches, which suggests that niche based processes (species sorting) could play a major role in organising chironomid metacommunities (Cottenie; 2005; Van der Gucht et al., 2007).

Concerning the outstanding role of environmental heterogeneity in metacommunity processes (Leibold et al., 2004; Heino et al., 2015), it is not surprising that its effect could also be captured in relative patterns of pairwise beta diversity components in all three chironomid metacommunities using both the POD and BAS approaches. This finding supports that environmental heterogeneity influences not only the variability of local assemblages, but it also affects the relative roles of underlying mechanisms related to species replacement and richness difference. Replacement and richness difference or nestedness resultant components of beta diversity are influenced by different ecological processes and thus generally relate to different environmental and spatial attributes as well (e.g. Boieiro et al., 2013; Legendre, 2014; Lewis et al., 2016; Gianuca et al., 2017). Below, we give several examples how components of pairwise beta diversity can be associated with different environmental and/or spatial gradients in the studied systems.

In the studied lake system, most chironomid taxa are associated with the littoral zone, while the offshore area is quite species poor (Árva et al., 2015a). Therefore, it is not surprising that vectors of the richness difference component of the POD and nestedness resultant component of the BAS approaches coincided with between site differences in water depth and variables representing distances from particular elements of the littoral zone (e.g. distances from the shore line, reed grass stand and submerged macrovegetation) in the RDA plot (Fig. 6a,d). On the other hand, the role of replacement component either using the POD or BAS approach increased with between site differences of environmental attributes that proved to be important to differentiate between the four main chironomid assemblage clusters in the lake, such as: (1) northern macrophyted littoral and sheltered boat harbours with silt sediment and high LOI550, (2) ripraps (rocks) with algal coating, (3) open water with silt sediment and low LOI550, and (4) southern littoral with sand sediment and low LOI550 (Árva et al., 2015a). The high congruency in response of species distribution patterns and beta diversity components to environmental gradients could be owing to markedly separated habitat types and related ecological processes in Lake Balaton. In the studied wetland, both micro- and meso-scale environmental heterogeneity is so high that neither habitats nor chironomid assemblages form clear clusters (Árva et al., 2017). This diverse patterning and probable complexity of the underlying ecological mechanisms could be the reason why relative importance of beta diversity components did not provide clear relationship with the considered environmental predictors. Moreover, the only clear congruence between the POD and BAS approaches was that increasing replacement was associated with the difference in presence of rock at compared sites (Fig. 6b,e). Rocks placed to some flow exposed sections represent unique, artificial habitats in this system. Since rocks have dense algal coating and consequently better oxygen supply than other substrates, they are inhabited by chironomid taxa which are not characteristic in other habitats of this wetland area (Árva et al., 2017). Further, in wetland, richness difference component of the POD approach tended to increase with increasing difference in water depth between the sites (Fig. 6b) due to the lower number of chironomid taxa in deeper habitats. This is likely in response to lower number of ecological niches in the deeper and less heterogeneous open water environment similarly to lake. In stream network, richness difference component of the POD and nestedness resultant component of the BAS approach were associated with increasing difference in the ratio of fine particle decomposing organic matter in the sediments (Fig. 6c,f). In addition replacement component was associated with differences in a series of environmental properties like sediment physical structure, stream width and dissolved oxygen content in both approaches. Overall these findings indicate that a multitude of environmental gradients influence patterns of species replacements and richness difference or nestedness resultant components of beta diversity in chironomid metacommunities. This patterning is in agreement with relative abundance based constrained assemblage patterns in the region (Árva et al., 2015a, 2017; Schmera et al., 2018) and emphasises the prominent role of habitat structure and range of food resource in the organization of chironomid metacommunities.

Components of beta diversity may be structured spatially even besides the effect of spatially structured environmental filters. For instance, Boieiro et al. (2013) identified strong pure spatial effect in both the replacement and richness difference components of POD when examined the beta diversity of ground beetles in Madeira Island Laurisilva. Carvalho & Cardoso (2014) provided another example of how the components of beta diversity change with dispersal possibilities. They revealed that variation in community composition of spiders was related mainly to replacement in case of good dispersers and to richness difference in dispersal-limited taxa using POD. In the latter group, geographical distance was an important predictor of between community dissimilarity (beta diversity). In our study systems spatial effect was the least important in lake, where the dominance of open water habitat enables relatively free dispersal for flying imagos. Further, the unique environmental conditions in the littoral zone favour an efficient environmental filtering and also antagonize potential colonization of abundant open water species. On the other hand the heterogeneous landscape of wetland including also variable areas of terrestrial habitats and unevenly distributed patches of tall trees and clamps may represent spatially structured dispersal constraints for chironomids (Delettre et al., 1992), and result a more pronounced spatial structure in pairwise assemblage composition relationships as well (c.f. Kärnä et al., 2015). Whereas, the country-wide stream network system covers the largest area and the most heterogeneous landscape, therefore it is not surprising that this metacommunity proved to be most structured spatially.

There is a yet not fully disentangled variability in dispersal of different macroinvertebrate groups in concern to what extent their movement happens overland or along watercourse

(Grönroos et al., 2013; Kärnä et al., 2015; Schmera et al., 2018). Here we obtained a better explanatory power for along water course spatial predictors (wPCNMs) than for predictors defined based on overland distances (aPCNMs) for beta diversity patterns in stream network. Although there are indications that dispersal of chironomids and several other flyable aquatic macroinvertebrates may be more confined to movement along the watercourse in habitats bordered by tall forest vegetation, in general these organisms are known to disperse quite effectively overland as well (Delettre et al., 1992; Armitage, 1995; Delettre & Morvan, 2000). On the other hand, in streams eggs and larvae of chironomids are also distributed by the water current (Pinder, 1995), which may emphasize the importance of watercourse distribution over overland dispersal. In fact, further research is needed to evaluate whether this observed pattern has a valid background from dispersal behaviour of chironomids or not. Since environmental properties themselves are often spatially structured, it is not rare that identified environmental and spatial effects overlap as well (Gilbert & Bennett, 2010; Legendre & Legendre, 2012). However, results of the variation partitioning prove that in our systems the overlap between the identified environmental and spatial effects is only moderate.

Conclusions

We demonstrated that both beta diversity and its replacement component increased in chironomid metacommunities from environmentally less heterogeneous lake, through more complex wetland to extended stream network ecosystem. Results proved that the relative role of metacommunity assembly mechanisms related to species replacement and richness difference or nestedness resultant components of beta diversity could also vary substantially across ecosystems in chironomids. We found that environmental heterogeneity and spatial processes explain some variation of the patterns of pairwise beta diversity components in chironomid metacommunities, and the most influential environmental attributes in this regard could be the habitat structure and the range of food resource. However, the wider applicability of beta diversity components is still hampered by the limits of particular indexes and the discrepancies between the results of concurrent approaches. Given the substantial differences between the interpretations of species replacement by the POD and BAS approaches, further research is needed to clarify which of the approaches should be preferred to assure general comparability over a wide-range of studies.

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Figure captions

Fig. 1 Location of Lake Balaton, Kis-Balaton wetland and sampled stream sites (○) in Hungary. Detailed maps of the distribution of sampling sites within Lake Balaton and Kis-Balaton wetland is provided in Árva et al. (2015a) and Árva et al. (2017), respectively.

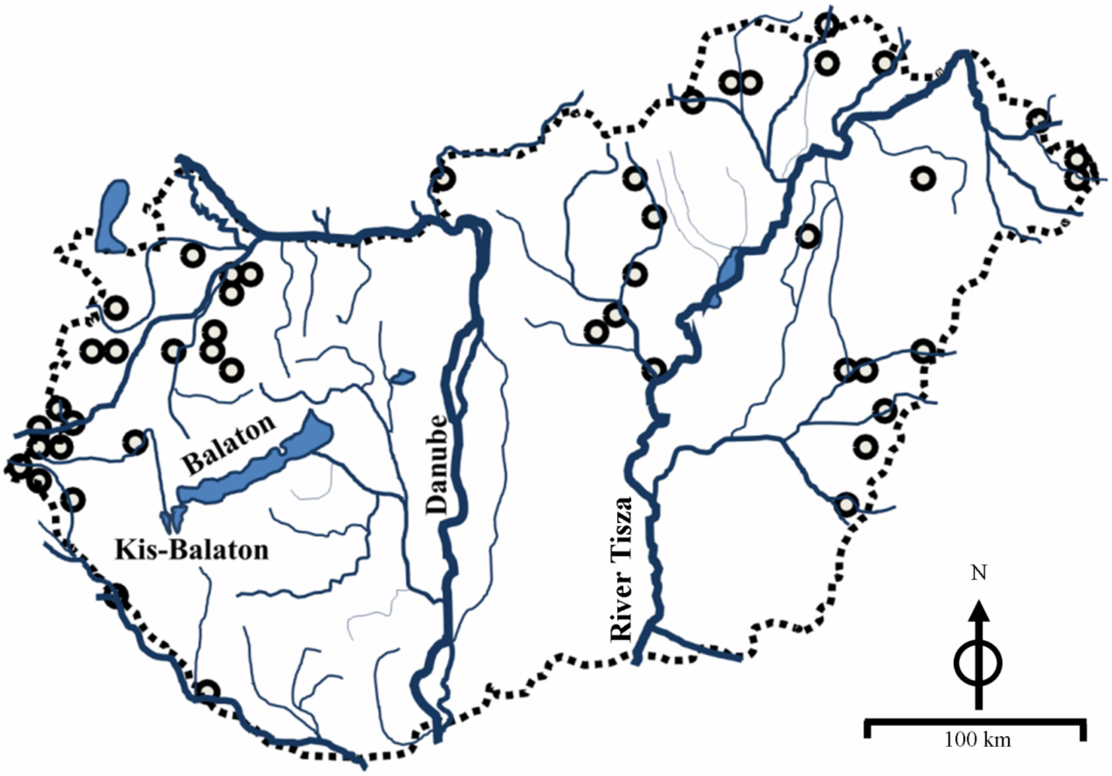
Fig. 2 Rarefied number of taxa of chironomids as a function of individuals sampled in lake, wetland and stream network ecosystems.

Fig. 3 Non-metric multidimensional scaling plot of sites of lake, wetland and stream network ecosystems based on their chironomid assemblages and the Jaccard dissimilarity index. Ninety five percent ellipses are shown for each ecosystem.

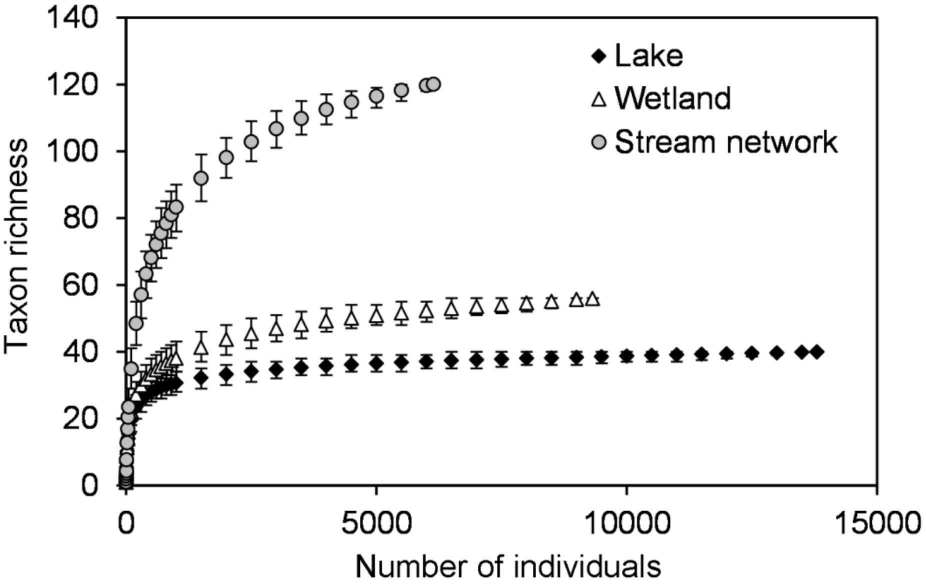
Fig. 4 Simplex ternary plots presenting pairwise presence-absence species relationships of chironomid metacommunities in lake (a, d), wetland (b, e) and stream network (c, f) ecosystems based on the Podani & Schmera (2011; POD; a-c) and Baselga (2012; BAS; d-f) approaches. Black dots represent relativized pairwise scores for all possible site combinations, and large grey circles indicate score centroids. Note that many points on the plots are overlapping due to the discrete values and limited number of possible score combinations.

Fig. 5 The relative roles of environmental and spatial effects in shaping pairwise beta diversity components of chironomid metacommunities in lake, wetland and stream network ecosystems according to the results of variation partitioning based on the Podani & Schmera (2011; POD) and Baselga (2012; BAS) approaches. In lake and wetland spatial variables were derived from between sites overland distance matrixes (aPCNM), while in stream network separate RDA models were composed based on spatial variables derived from between sites overland and watercourse distance (wPCNM) matrixes.

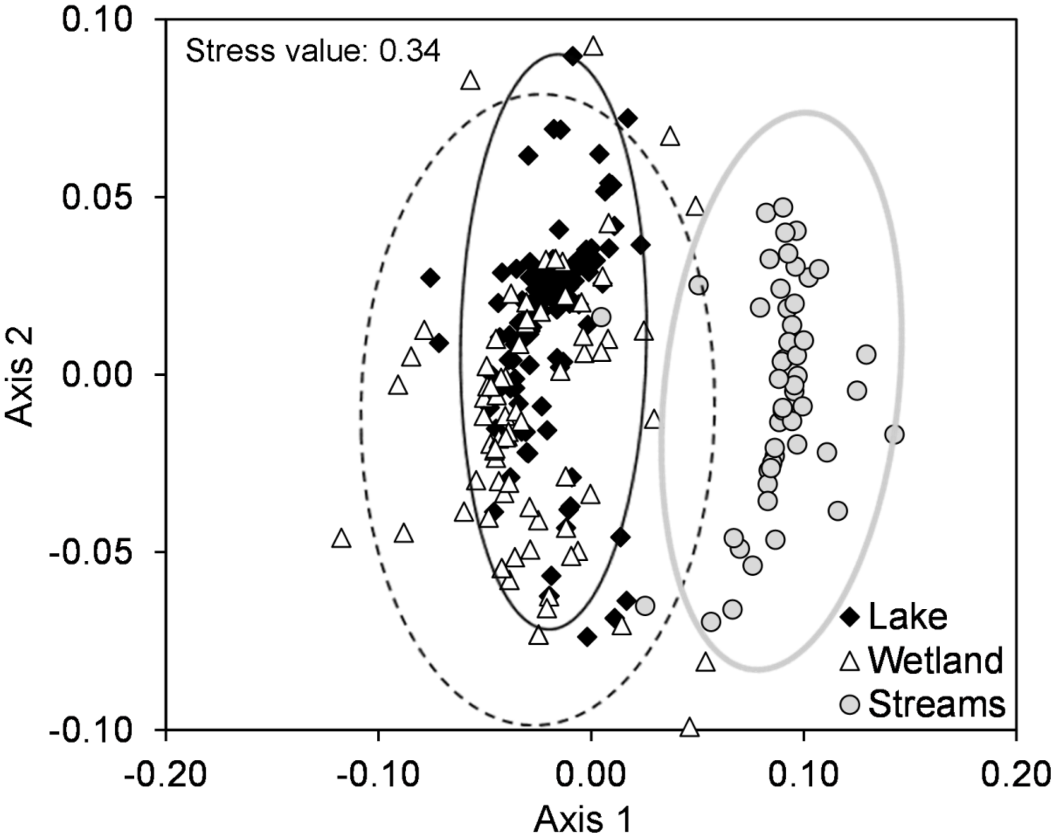
Fig. 6 Redundancy analysis (RDA) biplots showing the relation between pairwise beta diversity components of chironomid metacommunities according to the Podani & Schmera (2011; POD; a-c) and Baselga (2012; BAS; d-f) approaches and between sites differences in environmental properties (i.e. altitude, climatic, landscape, and local physical-, chemical- and biotic habitat attributes) and spatial variables (PCNM) in lake (a, d), wetland (b, e) and stream network (c, f) ecosystems. Red circles represent pairwise assemblages similarity (S_J) and beta diversity components ($Repl_{JP}$ and $Rich_{JP}$ in the POD, and $Repl_{JB}$ and $Nest_{JB}$ in the BAS approaches), black arrows represent between sites differences in specific environmental properties (abbreviations are explained in Appendix A in the Electronic Supplementary Material), while green arrows represent between sites differences in spatial variables based on overland (aPCNM; in lake and wetland) and water course (wPCNM; in stream network) distances. Note that for clarity we show only the most influential explanatory variables which correlate at r>0.15 with either of the first two RDA axes.



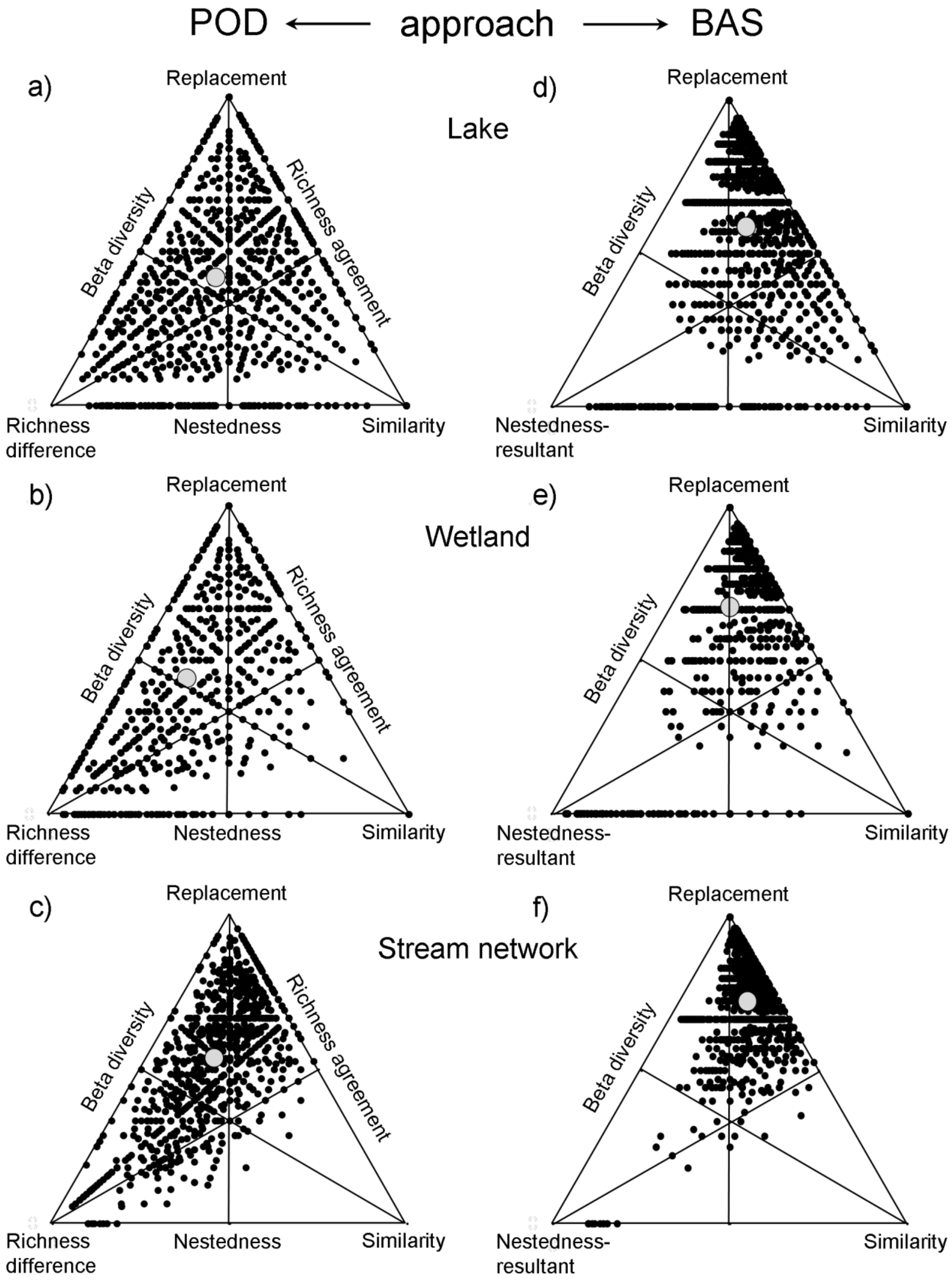
969

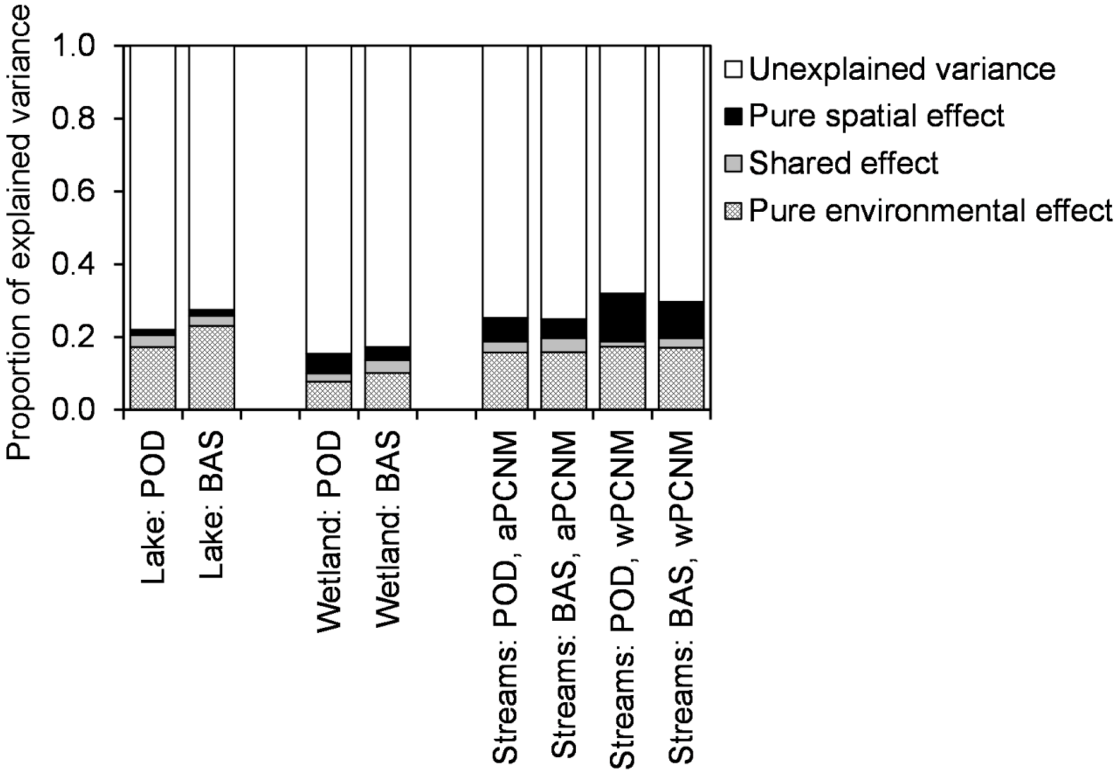


140
120
100
80
60
40
20
0
Taxon richness
0
5000
10000
15000
Number of individuals
◆ Lake
△ Wetland
● Stream network


Stress value: 0.34
Axis 2
Axis 1
0.10
0.05
0.00
-0.05
-0.10
-0.20
-0.10
0.00
0.10
0.20
Lake
Wetland
Streams

971


POD ⟵ approach ⟶ BAS
a)
Replacement
Beta diversity
Richness agreement
Richness difference
Nestedness
Similarity
Lake
d)
Replacement
Beta diversity
Nestedness-resultant
Similarity
b)
Replacement
Beta diversity
Richness agreement
Richness difference
Nestedness
Similarity
Wetland
e)
Replacement
Beta diversity
Nestedness-resultant
Similarity
c)
Replacement
Beta diversity
Richness agreement
Richness difference
Nestedness
Similarity
Stream network
f)
Replacement
Beta diversity
Nestedness-resultant
Similarity


Proportion of explained variance
1.0
0.8
0.6
0.4
0.2
0.0
Lake: POD
Lake: BAS
Wetland: POD
Wetland: BAS
Streams: POD, aPCNM
Streams: BAS, aPCNM
Streams: POD, wPCNM
Streams: BAS, wPCNM
☐ Unexplained variance
■ Pure spatial effect
▨ Shared effect
▨ Pure environmental effect

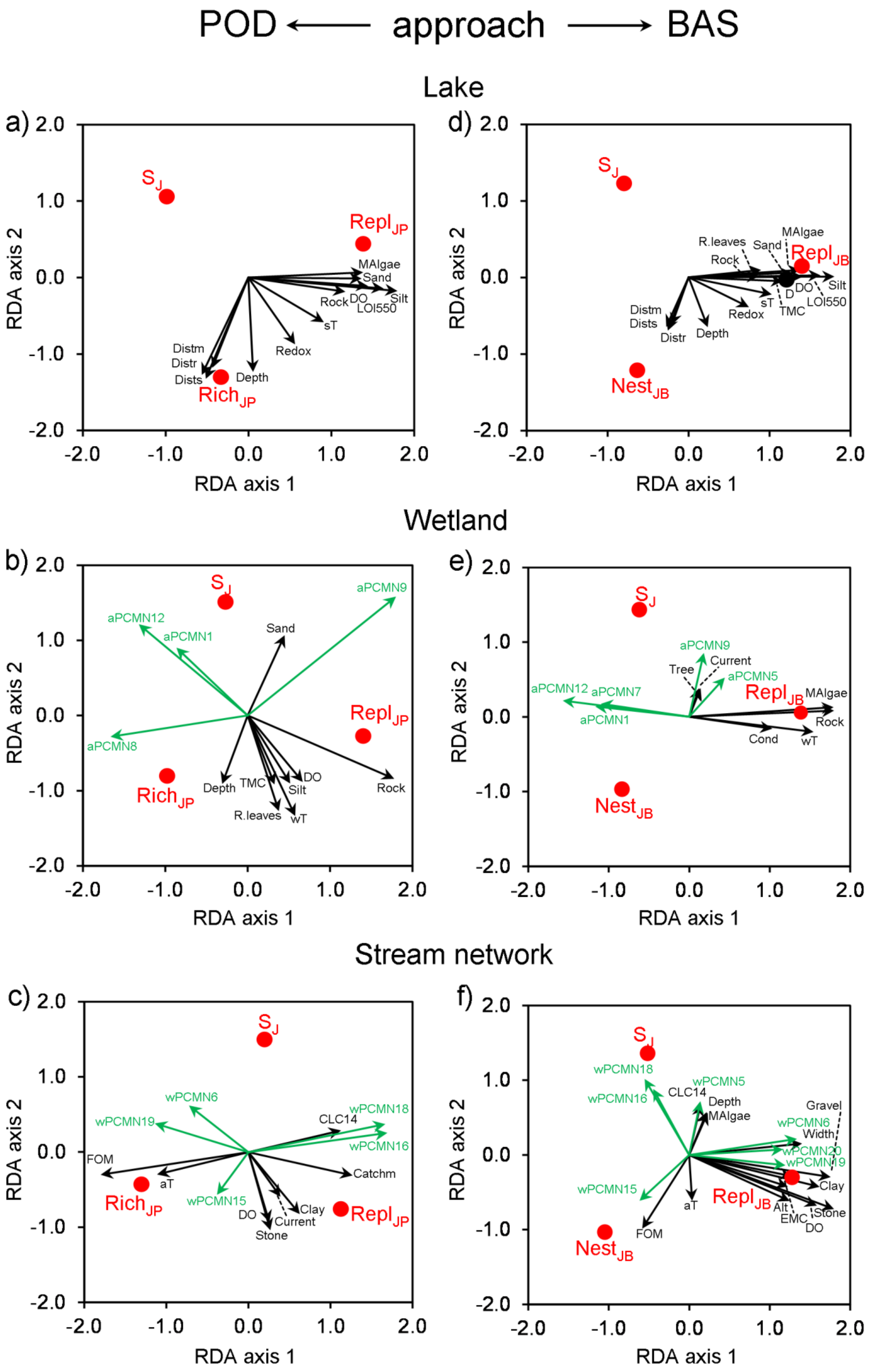

POD ← approach → BAS
Lake
a)
S_J
$Repl_{JP}$
$Rich_{JP}$
MAlgae
Sand
Rock
DO
Silt
LOI550
sT
Redox
Depth
Distm
Distr
Dists
d)
S_J
$Repl_{JB}$
$Nest_{JB}$
MAlgae
R.leaves
Sand
Rock
DO
D
Silt
LOI550
sT
TMC
Redox
Distm
Dists
Distr
Depth
Wetland
b)
S_J
$Repl_{JP}$
$Rich_{JP}$
aPCMN9
aPCMN12
aPCMN1
aPCMN8
Sand
Rock
DO
Silt
TMC
Depth
R.leaves
wT
e)
S_J
$Repl_{JB}$
$Nest_{JB}$
aPCMN9
Current
Tree
aPCMN5
aPCMN12
aPCMN7
aPCMN1
MAlgae
Rock
Cond
wT
Stream network
c)
S_J
$Repl_{JP}$
$Rich_{JP}$
wPCMN6
wPCMN19
wPCMN18
wPCMN16
wPCMN15
CLC14
FOM
aT
Catchm
Clay
Current
DO
Stone
f)
S_J
$Repl_{JB}$
$Nest_{JB}$
wPCMN18
wPCMN5
wPCMN16
CLC14
Depth
MAlgae
Gravel
wPCMN6
Width
wPCMN20
wPCMN19
Clay
wPCMN15
aT
Alt
EMC
Stone
DO
FOM
RDA axis 1
RDA axis 2
-2.0
-1.0
0.0
1.0
2.0

Table 1 Multiple-site Jaccard dissimilarity (multiple-D_J; total beta diversity), species replacement (multiple-$Repl_{PJ}$) and richness difference (multiple-$Rich_{PJ}$) *sensu* Podani & Schmera (2011) calculated according to Ensing & Pither (2015), and species replacement (multiple-$Repl_{BJ}$) and nestedness resultant (multiple-$Nest_{BJ}$) components *sensu* Baselga (2012) of beta diversity in chironomid metacommunities of lake, wetland and streams network ecosystems. In lake and wetland ecosystems, index values (mean and 95% CI) were also assessed based on 1000 random subsamples of 50 sites corresponding the number of effective samples (i.e. sites with chironomids; *n*) in the stream network system as suggested by Baselga (2010).

	Lake		Wetland		Stream network
	total sample *n*=128	resampled to *n*=50) mean (95% CI)	total sample *n*=76	resampled to *n*=50 mean (95% CI)	total sample *n*=50
multiple-D_J	0.987	0.969 (0.967-0.972)	0.984	0.976 (0.975-0.977)	0.976
multiple-$\mathrm{Repl}_{\mathrm{PJ}}$	0.547	0.537 (0.483-0.595)	0.517	0.513 (0.462-0.574)	0.648
multiple-$\mathrm{Rich}_{\mathrm{PJ}}$	0.440	0.433 (0.377-0.485)	0.466	0.433 (0.402-0.486)	0.328
multiple-$\mathrm{Repl}_{\mathrm{BJ}}$	0.977	0.946 (0.941-0.952)	0.969	0.956 (0.951-0.961)	0.964
multiple-$\mathrm{Nest}_{\mathrm{BJ}}$	0.009	0.023 (0.018-0.028)	0.014	0.021 (0.016-0.025)	0.012

Table 2 Mean and median (in brackets) values of pairwise Jaccard similarity (S_J), species replacement ($Repl_{PJ}$) and richness difference ($Rich_{PJ}$) *sensu* Podani & Schmera (2011; POD), and species replacement ($Repl_{BJ}$) and nestedness resultant ($Nest_{BJ}$) components *sensu* Baselga (2010; BAS) of beta diversity in chironomid metacommunities of lake, wetland and streams network ecosystems (see also Fig. 4). Among ecosystems variability in each measure was inspected by permutational one-way analysis of variance (pANOVA) and permutational *t* post-hoc test; values differing in their superscription letters are different at $P<0.05$. Differences between the two coherent components of beta diversity was analysed also with permutational *t*-test in each metacommunities and separately for the POD and BAS approaches; values differing in their superscription numbers are different at $P<0.05$.

	Lake	Wetland	Stream network	pANOVA	
	mean (median)			*F*	*P*
S_J	0.254^{a} (0.235)	0.163^{b} (0.143)	0.187^{c} (0.182)	444	0.001
Repl_{PJ}	$0.416^{a,1}$ (0.400)	$0.441^{b,1}$ (0.444)	$0.538^{c,1}$ (0.571)	138	0.001
Rich_{PJ}	$0.330^{a,2}$ (0.308)	$0.396^{b,2}$ (0.375)	$0.276^{c,2}$ (0.238)	146	0.001
Repl_{BJ}	$0.587^{a,1}$ (0.615)	$0.675^{b,1}$ (0.750)	$0.725^{c,1}$ (0.750)	218	0.001
Nest_{BJ}	$0.158^{a,2}$ (0.092)	$0.162^{a,2}$ (0.067)	$0.088^{b,2}$ (0.051)	75	0.001

Table 3 Significances (*F* and *P* are indicated) and percentage explanatory powers (adjusted R^2 values) of full (i.e. with all significant explanatory variables retained during the forward stepwise selection procedure at $P<0.05$) and partial (i.e. separately for each individual variable groups with retained significant variables) redundancy analysis (RDA) models by explanatory variable groups constructed to evaluate variability in pairwise beta diversity components of chironomid metacommunities in lake, wetland and stream network ecosystems based on the approaches of Podani & Schmera (2011; POD) and Baselga (2012; BAS).

Explanatory variable groups	POD				BAS			
			Explained variance				Explained variance	
	F	*P*	Total (%)	Pure effect (%)	*F*	*P*	Total (%)	Pure effect (%)
Lake								
I. Altitude	-	-	-	-	-	-	-	-
II. Catchment	-	-	-	-	-	-	-	-
III. Climate	-	-	-	-	-	-	-	-
IV. Landscape	68.7	<0.001	4.8	1.6	72.5	<0.001	7.4	1.8
V. Physical	187.3	<0.001	10.3	3.7	263.2	<0.001	13.9	4.1
VI. Chemical	118.7	<0.001	6.8	1.8	167.6	<0.001	9.4	1.7
VII. Plant and organic matter	113.1	<0.001	8.9	3.6	164.4	<0.001	12.4	4.3
VIII. aPCNM	27.3	<0.001	4.8	1.5	23.3	<0.001	4.4	1.5
Full model	60.0	<0.001	22.0		72.6	<0.001	27.4	
Wetland								
I. Altitude	-	-	-	-	-	-	-	-
II. Catchment	-	-	-	-	-	-	-	-
III. Climate	-	-	-	-	-	-	-	-
IV. Landscape	14.8	<0.001	1.0	0.6	28.7	<0.001	2.0	1.2
V. Physical	16.1	<0.001	4.3	3.0	33.7	<0.001	4.5	1.2
VI. Chemical	15.6	<0.001	1.6	0.4	37.8	<0.001	3.8	1.1
VII. Plant and organic matter	12.5	<0.001	3.8	3.1	29.2	<0.001	8.5	3.9
VIII. aPCNM	26.4	<0.001	7.7	5.4	25.5	<0.001	7.1	3.6
Full model	16.6	<0.001	15.4		20.9	<0.001	17.2	
Stream network based on overland distances								
I. Altitude	-	-	-	-	24.5	<0.001	0.020	0.003

II. Catchment	21.6	<0.001	1.7	0.4	-	-	-	-
III. Climate	16.8	<0.001	1.4	0.9	4.8	0.011	0.4	0.3
IV. Landscape	11.2	<0.001	2.7	2.6	8.0	<0.001	2.6	1.6
V. Physical	8.3	<0.001	3.3	3.9	20.3	<0.001	9.1	4.7
VI. Chemical	9.9	<0.001	3.9	3.7	12.9	<0.001	4.1	3.0
VII. Plant and organic matter	25.2	<0.001	4.0	5.5	11.5	<0.001	3.6	3.1
VIII. aPCNM	12.7	<0.001	9.5	6.5	11.1	<0.001	9.1	5.2
Full model	14.9	<0.001	25.2		12.7	<0.001	24.9	
Stream network based on watercourse distances								
I. Altitude	-	-	-	-	24.5	<0.001	2.0	0.6
II. Catchment	21.6	<0.001	1.7	0.3	-	-	-	-
III. Climate	16.8	<0.001	1.4	1.4	4.8	0.011	0.4	0.5
IV. Landscape	11.2	<0.001	2.7	5.4	8.0	<0.001	2.6	2.8
V. Physical	8.3	<0.001	3.3	2.9	20.3	<0.001	9.1	4.9
VI. Chemical	9.9	<0.001	3.9	3.4	12.9	<0.001	4.1	3.0
VII. Plant and organic matter	25.2	<0.001	4.0	3.0	11.5	<0.001	3.6	1.8
VIII. wPCNM	18.9	<0.001	14.6	13.2	11.5	<0.001	12.5	9.9
Full model	20.0	<0.001	31.9		14.3	<0.001	29.6	

aPCNM and wPCNM are spatial variables derived from principal coordinate analysis of neighbouring matrix using logarithmic transformed between sites overland distances and watercourse distances, respectively.