

Seasonal changes in relative contribution of environmental control and spatial structuring on different dispersal groups of stream macroinvertebrates

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Abstract

The role of environmental control and spatial structuring may vary depending on dispersal mode within a metacommunity in stream systems. However, as a result of high seasonal variation in environment conditions and phenological features, there might be considerable seasonal changes in the relative importance of structuring factors. The objective of this study was (i) to determine the relative role of structuring factors for aquatic macroinvertebrates with different dispersal mode groups which have seasonal variation in their dispersal capacity and (ii) to disentangle seasonal changes in metacommunity structuring. We sampled 50 stream sites of the Middle Danube Basin (Hungary) in spring and summer. We compared Distance–Decay Relationships between communities of different dispersal groups and distance measures, and then we used variation partitioning analysis and Moran’s eigenvector maps based on overland and watercourse distances to reveal structuring processes in both seasons. We found that metacommunities of all dispersal groups were influenced in both seasons mainly by environmental factors with additional impacts of the spatial components. Our findings suggest that metacommunities of taxa with temporally stable dispersal capacity have seasonally stable structuring processes, while the relative importance of structuring factors can vary seasonally in groups with seasonally changing dispersal capacity.

Keywords

Active and passive dispersals, Overland and watercourse distances, Metacommunity, Stream ecosystems, Community structure

Introduction

Biotic communities cannot be considered as isolated entities, but rather as parts of a network of communities in which the rate of dispersal has a pronounced impact on species composition and community dynamics. Estimating the relative importance of local (e.g., environmental filtering) and regional factors (e.g., dispersal based processes) simultaneously with spatial variation is the main focus of metacommunity ecology (Leibold et al., 2004), which is one of the most intensively developing branches of community ecology (e.g., Holyoak et al., 2005; Erős et al., 2012; Cañedo-Argüelles et al., 2015; Heino et al., 2015a; Tonkin et al., 2017).

In riverine ecosystems, metacommunity paradigms (Leibold et al., 2004; Logue et al., 2011) are not mutually exclusive, and communities are structured by a combination of spatial and environmental processes (Erős et al., 2012; Winegardner et al., 2012; Grönroos et al., 2013; Tonkin et al., 2017).

As a result of high seasonal variation in environmental conditions among habitats having different quality, there might be considerable changes in the relative importance of spatial and environmental variables structuring metacommunities in stream systems (Erős et al., 2012; Fernandes et al., 2014; Heino et al., 2015a). Environmental and spatial factors act differently for taxa with different dispersal abilities (Brown & Swan, 2010; Grönroos et al., 2013; Cañedo-Argüelles et al., 2015; Tonkin et al., 2017; Schmera et al., 2018). In this regard, macroinvertebrates are often classified into different groups based on their dispersal capacities, which may aid our understanding of their metacommunity organization (e.g., Brown & Swan, 2010; Kärnä et al., 2015; Razeng et al. 2016; Schmera et al., 2018). The most often used system distinguishes three main dispersal groups of macroinvertebrates as follows: aquatic passive (AqPa), terrestrial passive (TePa) and terrestrial active (TeAc) (Grönroos et al., 2013; Heino, 2013).

Movement between habitat patches can present seasonally different challenges to dispersal groups due to the differences in their phenological features. Thus, dispersal groups can give different responses to the seasonal changes under environmental conditions. However, heterogeneity of dispersal capacity of aquatic macroinvertebrates appears not only in their phenological stages and morphological structures but also in the seasonality of their dispersal patterns (Fig. 1) (e.g., Bilton et al., 2001; Csabai et al., 2012; Boda & Csabai, 2013). The seasonal differences in the way and mode of movement between dispersal mode groups have important consequences for processes of metacommunity structuring. Interestingly, so far only few studies have dealt with the temporal aspects of metacommunity structuring of

stream macroinvertebrate communities and its determining factors (Göthe et al., 2013; Sarremejane et al., 2017).

This study aims to determine the relative role of environmental and spatial controls on aquatic macroinvertebrate metacommunities, which differ in their dispersal abilities. We compared the distance–decay relationships (DDRs) between the community similarity of different dispersal groups (AqPa, TePa and TeAc) using two different distances (overland and watercourse) in each season separately (summer and spring). We also examined the differences between the relative contribution of spatial structuring and environmental control on different dispersal groups. We made the following predictions:

- (1) Due to their limited and seasonally constant dispersal capacity (Fig. 1), AqPa metacommunities are under high and stable spatial control. Therefore, they show strong DDRs indicating dispersal limitation. Underwater (or waterway) dispersal of AqPa is directional and common among wingless aquatic macroinvertebrates. Therefore, we predicted that measuring watercourse distances will be a better predictor than overland distances in both seasons.
- (2) TePa species have aquatic larvae with low dispersal capacity in spring and winged adults with moderate dispersal capacity in summer (Fig. 1). Thus, we predicted a seasonal difference in metacommunity structuring. We predicted spatial control in spring, increasing environmental control in summer and moderate DDRs in both seasons. We also predicted that overland distances will be better predictors in spring, while watercourse distances will be better predictors in summer.
- (3) Dispersal of TeAc species mostly occurs when overwintered adults disperse extensively, or when the new generation becomes mature and emerges from the water. The water-seeking flight is considered as a synchronized and species-specific phenomenon for Odonata and Trichoptera, while for Coleoptera and Heteroptera, it is a year-long presence in the air with seasonally changing abundance (Fig. 1). Because TeAc should be able to find proper habitat by self-generated and well-controlled flight through the landscape, we predicted strong environmental control in both seasons and therefore that the overland distances will be better predictors in both seasons than water- course distances.

Materials and methods

Study sites

Fifty stream sites were selected in the middle Danube River catchment, Hungary. During the research planning process (e.g., pre-selection of the sampling sites), special attention was paid to avoid large artificial barriers (e.g., large reservoir dams) above the sampling sites. Consequently, all sampled sites can be considered as natural or near-natural. Altogether 50 stream sites were sampled (Fig. 2) in the summer of 2013 (August) during relatively low water level conditions, and in the spring of 2014 (March and early April). Note, that seasonal samples were collected in consecutive years, because prolonged high flow prevented effective sampling in the spring of 2013.

Climate and seasonal variations in Hungary

The climate of Hungary is mostly determined by the combined effect of its low elevation (situated in the Carpathian Basin surrounded by mountain ranges) and its location (in Central Europe where the effects of different climatic zones overlap). The climatic conditions are influenced by the humid oceanic climate with small variation in temperature and evenly dispersed precipitation and the less humid continental climate with a larger yearly variation in temperature and moderate precipitation. Furthermore, due to the Mediterranean effect the annual mean temperature is between 9 and 11°C, which is 2.5°C higher than the typical value at the same latitude (Mezősi, 2016). The annual mean precipitation is between 550 and 650 mm and the average annual sunshine hours vary between 1740 and 2080 (mean annual values were derived from meteorological recordings between 1901 and 2014; MET1, 2018; MET2, 2018).

Climatic conditions are characterized by four distinct seasons (Mezősi, 2016). Here only the climatic conditions in spring and summer are described corresponding to our sampling. The first part of spring has a winter character with cold temperatures and occasional snow cover. In the spring of 2014, the annual mean temperature was 12.1°C, which is 1.8°C higher than the average between 1901 and 2011 (MET3, 2018). The majority of the precipitation is falling between May and July. In the summer of 2013, due to the Mediterranean effect the average annual temperature was 21.7°C, which is 1.5°C higher than the average between 1901 and 2011 (MET3, 2018). The daily maximum temperature often exceeds 35°C, especially in July and August becoming the warmest period in the year. Therefore, the end of summer is characterized by lower water levels and desiccated streambeds.

Sampling of biological elements

Macroinvertebrates were sampled using a standard hand net with a frame width of 25 cm and mesh size of 1000 μ m partially (see sorting) following the multi-habitat sampling technique described by the AQEM Consortium (2002) and by Hering et al. (2003). The substrate was disturbed in a 0.25 X 0.25 m area upstream of the net within a depth of at least 10–15 cm. According to the protocol, one sample consisted of 20 representative sampling units from the dominant (> 5% coverage) microhabitat types of the sampling site. Collected samples were preserved in the field and later, unlike the AQEM protocol, were completely sorted in the laboratory, therefore, all specimens were sorted from the samples. Individuals of macroinvertebrates from 12 taxonomic groups (Gastropoda, Bivalvia, Hirudinea, Crustacea, Ephemeroptera, Odonata, Plecoptera, Heteroptera, Coleoptera, Megaloptera, Trichoptera, and Diptera including Chironomidae) were identified under a stereomicroscope to the possible lowest taxonomic level (mainly to species, species group or at least genus level except for Diptera). Identified macroinvertebrate specimens were preserved in 70% alcohol. All the collected and identified specimens are deposited in ethanol in the Collection of MTA Centre for Ecological Research, Danube Research Institute, Department of Tisza Research, Hungary.

Definitions of dispersal mode groups

Our knowledge on the biology of dispersal of most macroinvertebrate taxa is generally insufficient, therefore, macroinvertebrates were sorted into three dispersal mode groups following the typology suggested by Heino (2013) and have been extended based on the collected taxonomic groups in the field. (1) Species with aquatic larvae and adult stages, which have a passive underwater dispersal strategy (Aquatic passive, AqPa: Gastropoda, Bivalvia, Hirudinea, Crustacea); (2) Species with aquatic larvae and terrestrial winged adults (Terrestrial passive, TePa: Diptera with small body size [Ceratopogonidae, Chironomidae, Culicidae, Dixidae, Simuliidae]), note that because of the limited ability of winged adults, these taxa can only disperse passively over the landscape by wind or via animal vectors (Bilton et al., 2001; Trájer et al., 2017); (3) species with aquatic larvae and actively dispersing terrestrial adults, which can change the direction of flying deliberately (Terrestrial active, TeAc: Ephemeroptera, Odonata, Plecoptera, Heteroptera, Coleoptera, Megaloptera, Trichoptera and Diptera with large body size [Tipuloidea, Ptychopteridae, Stratiomyidae, Athericidae, Rhagionidae, Tabanidae, Empididae, Muscidae, Scathophagidae, Ephydriidae]).

Spatial variables

Spatial variables were assessed using Moran's eigenvector map analysis (MEM; Dray et al., 2006, 2012), which is a generalization of the Principal coordinates of neighbour matrices (PCNM) approach (Griffith & Peres-Neto, 2006). This approach is widely used for modelling spatial structures in biological communities (e.g., Heino & Alahuhta, 2015; Sály & Erős, 2016; Tolonen et al., 2018). First, the pairwise spatial distance matrix of sampling sites was calculated. Both overland and watercourse distances were calculated because the dispersal routes can vary among the different dispersal mode groups (Astorga et al., 2012; Göthe et al., 2013; Grönroos et al., 2013; Kärnä et al., 2015). Overland distance refers to the shortest distance between two sampling sites, while watercourse distance takes into consideration the real length of the connected water courses between the sites. Geographical distances between each pair of sampling sites were calculated in QGIS (Quantum GIS Development Team, 2010). In the second step, we summarized the adjacency of the assemblages by assigning ones and zeros to each pair of sampling sites in the symmetrical binary matrix (connectivity matrix-CM), with ones for neighbouring sites and zeros otherwise (Dray et al., 2012). To obtain this neighbourhood of sampling sites we applied a minimum spanning tree (MST) algorithm. Two sites were considered neighbours when their distance was lower than the maximum distance value between two connected sites in the MST. In the third step, the distance matrix of sampling sites was transformed into a weighted distance matrix (WM) using the following formula (Dray et al., 2006):

$$S_{ij} = 1 - \left(\frac{D_{ij}}{\max(D_{ij})} \right),$$

where S_{ij} is the normalized distance for the distance of site i and site j ; D_{ij} is the overland or watercourse distance between site i and site j ; and $\max(D_{ij})$ is the maximum value of the overland or watercourse distance matrix. In the fourth step, CM was multiplied with WM to get a spatial weighting connectivity matrix, which compresses information about the strength of the potential interaction of assemblages between each pair of sampling sites (Dray et al., 2006). Finally, we calculated the eigenvectors of the spatial weighting connectivity matrix, which maximizes the Moran's index of autocorrelation using the 'space- makeR' package (Dray, 2013) in R ver. 3.3.3 (R Core Team, 2017).

Environmental variables

The key environmental attributes (water chemistry, microhabitat and streambed morphology, hydrological features, riparian vegetation and water-catchment characteristics) that generally influence aquatic communities in stream habitats (Allan & Castillo, 2007) were measured at

each site in both survey periods, except for catchment variables, which were assessed using geoinformatic databases or maps.

The following chemical and physical variables were measured: water temperature, pH, O₂, conductivity (using Hach HQ40d Portable MultiParameter Meter), NO₂⁻-N, NH₄⁺-N, P and PO₄³⁻-P (mg l⁻¹) using colorimetry (Hanna Checker HC HI700).

The dominant substrate types and the percentage of substratum cover were assessed visually, following the AQEM protocol (AQEM Consortium, 2002). Furthermore, the macroalgal and macrophyte cover- age were registered at each site, which were classified based on life-forms: emergent plant (%), submerged plant (%), floating leaved plant (%) and filamentous algae (%). The hydrological features of the sites were characterized by wetted width (m), depth (cm) and current velocity (cm/s). Water depth and current velocity were measured at 3–6 (varied according to the width) equally spaced points along each transect. Parameters of the catchment land cover, such as urban area (%), natural area (%), intensive agricultural area (%), non-intensive agricultural area (%) and land- use index were obtained from the CORINE land-cover database for Europe (CLC 2000, European Environment Agency). Altitude (elevation a.s.l, m) was measured in the field using a GPS device (Garmin Montana 650), while the size of catchment areas (km²) were calculated based on the ArcGIS Software (ver 10, ESRI).

Data analysis

We used ADONIS (Permutational Multivariate Analysis of Variance Using Distance Matrices) by Anderson (2001) in the “vegan” package (Oksanen et al., 2007) of R (R Core Team, 2017), a robust version of nonparametric permutational analysis of variance, with 999 permutations and the Bray–Curtis measure for testing differences in macroinvertebrate community structure among seasons (summer vs. spring). The calculation of the difference was made on the whole community and on all the three dispersal mode groups separately.

We used the Bray–Curtis similarity index for the distance–decay relationships (DDRs), which describes how the similarity in species composition between two communities varies with either geographical or water- course distance. The strength of the statistical relationship was quantified by the determination coefficient (R²) of a general linear regression model among the pairwise spatial distance and pairwise community distance and pairwise environmental distance matrices, respectively. Consequently, Mantel test was applied to examine the relationship between community similarity, spatial distance and environ- mental distance matrices separately. A significant relationship indicates the effect of environmental

heterogeneity on community structuring. The statistical analyses were performed in R (R Core Team, 2017) using the “vegan” package (Oksanen et al., 2007).

The environmental variables were tested for normality and transformed by natural logarithm or $\arcsin\sqrt{x}$ when the normality assumption was violated. After the transformations principal component analyses (PCA) were used for three sets (water chemistry, habitat morphology and hydrological features and catchment) of environmental variables (Table 1) to reduce the number of explanatory variables. All PCA axes explaining more than 10% were used for further analyses because they explained most of the variation, with only small increases for each remaining component afterwards (Plenzler & Michaels, 2015). The first two axes in all groups were retained from the variables in 2013: variables of water chemistry (explained variations: 60.67% and 19.09%), habitat morphology and hydrological variables (33.56% and 17.22%) and catchment variables (64.04% and 29.5%). The first three axes were retained from the variables of the water chemistry (47.33, 26.26 and 12.73%) and the habitat morphology groups (31.3, 17.39 and 10.56%) while the first two axes were retained from the catchment group in 2014 (64.03% and 29.5%). Then the PCA axes scores were used as explanatory variables for the further analyses. Hellinger transformation was used on the species data table (Legendre & Gallagher, 2001). Eigenvectors with positive eigenvalues (three from the overland distances and two from the watercourse distances) were used as spatial variables in further analyses (Dray et al., 2006). We used variation partitioning in Canoco 5.04 software (Braak & Šmilauer, 2012) to examine the relative importance of environmental and spatial variables in explaining variation in community structure. Thus, the total percentage of variation explained by variation partitioning is decomposed into pure and shared contributions of two sets of predictors (environmental [E] and spatial [S]). The main results provided by variation partitioning contained the following fractions: [E] variation explained only by environmental components, [S] variation explained only by spatial components, [shared, E + S] spatially structured environmental variation, and unexplained variation (Legendre et al., 2005; Heino et al., 2012). The pure environmental fraction indicates the importance of environmental filtering in metacommunity structuring. A high importance of spatial fraction suggests that either limiting or high dispersal rates are important for macroinvertebrate community structure (Cottenie, 2005; Ng et al., 2009).

The comparison of the distance measures (overland vs. watercourse) was conducted using the total spatial fraction (total spatial fraction = pure spatial [S] + shared fraction [E + S]). The higher the values of the total spatial fraction, the higher the explanatory power.

Results

General results

The ADONIS showed that the significance levels and the variance were explained by seasons for the whole community and the dispersal mode groups. Significant differences were found in the community structure of macroinvertebrates at the level of the entire community between seasons (Table 2). The effects of season were statistically significant for TePa and TeAc, but not for AqPa dispersal mode groups (Table 2). The pure environmental fraction [E] explained 3.5–15.6% of the variance. The pure spatial fraction [S] explained 2.1–5.4% of the variance (Supplementary Table 1).

Aquatic-passive dispersal mode group (AqPa)

There were significant but relatively weak DDRs using watercourse distance measure in both seasons, while we found no significant DDRs in spring using overland distances (Table 3). There were significant and strong positive relationships between AqPa community similarity and environmental similarity for both seasons (Adjusted R^2 in spring = 0.108, and in summer = 0.085) (Table 3). The correlations between biological and spatial distance matrices in both seasons were stronger using overland distances (Table 4). For AqPa, results showed significant effects of pure environmental fractions in both seasons, when using overland distances and both spatial and environmental controls, and when using watercourse distances. There were small differences between spring and summer in the explained variation. However, the relative roles of environmental and spatial fractions did not change (Fig. 3). Results of the variance partitioning largely changed when using different distance measures. However, there were only slight differences when comparing the total spatial fractions of the distance metrics in both seasons (Fig. 3). Results showed that overland distances were better predictors of the species composition than watercourse distances (Supplementary Table 2).

Terrestrial-passive dispersal mode group (TePa)

We found significant but relatively weak DDRs in spring for both distance measures, while no significant relationships were found in summer (Table 3). There were no significant relationships for spring, and significant but weak for summer between TePa community similarity and environmental similarity (Table 3). The correlations between biological and spatial distance matrices were stronger using overland distances in spring, but there were no significant relationships in summer (Table 4). In spring, TePa assemblages were under low

spatial control (2.8% of the explained variance), while in summer, a significant but weak environmental control was detected (4.9% explained variance) using overland distances. The joint effect of spatial and environmental control was replaced by environmental filtering from spring to summer, when watercourse distances were used (Fig. 3). Seasonal changes could be detected using either one of the distances. TePa had the smallest variance in their significant relationships compared to the other dispersal mode groups (Fig. 3). Results of the variance partitioning remained the same regardless of the distance metrics in summer (showing environmental control in both cases of distance metrics), but changed in spring (spatial control vs. total spatial fraction in case of the overland vs. the watercourse distance, respectively, see Fig. 3). Overland distances were better predictors of species composition than watercourse distances (Supplementary Table 2).

Terrestrial-active dispersal mode group (TeAc)

We found significant but relatively weak DDRs between TeAc summer community similarity matrix and both distances (watercourse and overland), and TeAc spring community similarity matrix and water- course distances. However, we found no evidence of significant DDRs in spring, using overland distances (Table 3). There were significant and strong positive relationships between TeAc community similarity and environmental similarity for both seasons (Adjusted R^2 in spring = 0.094, and in summer = 0.136) (Table 3). The correlations between biological and distance matrices were stronger when using overland distances in summer, but there were no significant relationships in spring (Table 4). For TeAc, results showed significant effects of both spatial and environmental controls in both seasons when using overland distances. Environmental control was prevalent in spring, but in summer, both spatial and environmental controls were detected when using watercourse distances (Fig. 3). Results of the variance partitioning remained the same regardless of the distance metrics in summer, but largely changed in spring (Fig. 3). Results show that overland distances were better predictors than watercourse distances (Supplementary Table 2).

Discussion

The aim of this study was to determine the relative importance of environmental and spatial control for aquatic macroinvertebrates with different dispersal modes and to disentangle seasonal changes in meta- community structuring.

We found no or weakly significant (with low total variance, < 1) distance–decay relationships (Table 3), which was also supported by Mantel tests (Table 4). This suggests that metacommunity structuring was not influenced by dispersal related processes in any dispersal mode groups in a biologically sensible manner (Erős et al., 2017). Possible reasons contributing to these results are the extent of the study area and the overarching role of environmental filtering over spatial factors (see below). Our study was restricted to a single ecoregion and a spatial scale of 5–1500 km. Within this ecoregion any species can occur at any site, and therefore, in the light of our results, it is likely, that their occurrence depends largely on environmental factors. Presumably, the examination of larger spatial gradients would have resulted in stronger DDRs (Erős et al., 2017).

Overall, the environmental filtering has been shown to have the highest relative role, but spatial control did also take part in shaping metacommunity structuring, which partially lines up with the findings of other studies on stream organisms (see Heino et al., 2015b; Tonkin et al., 2017). The relative importance of spatial and environmental factors may differ depending on the dispersal characteristics of organisms (e.g., De Bie et al., 2012), therefore we discuss patterns in different dispersal mode groups separately.

Aquatic-passive dispersal mode group (AqPa)

For AqPa, we expected dispersal limitation and therefore a strong and temporally stable spatial signal in both seasons (Fig. 4); however, we found both small spatial signal (5.4% and 3.9%) and higher environmental control (15.6% and 11.6%) when using water-course distances. The results were consistent with some previous studies, in which weak spatial control of organisms belonging to this group was found (Heino & Mykrä, 2008; Landeiro et al., 2012). On the other hand, we found a pure environmental control using overland distances (Fig. 4), which is in agreement with the observation of Grönroos et al. (2013), who also found evidence for pure environmental control for AqPa. These results suggest that the overland dispersal via animal vectors could be the predominant form of dispersal that was still highly underestimated by us, since we made our predictions based on the underwater movements of the group. However, if waterfowls have the potential to transport aquatic macroinvertebrates over several hundreds of kilometres in a random way (Van Leeuwen et al., 2012), spatial extent ceases to be an obstacle, and spatial signals will be weaker. Therefore, passive dispersal (presumably by waterfowls) exhibited less spatial control than what we expected. Overall, both the lack of spatial control and the low spatial fraction

suggest that dispersal limitation is less important for AqPa at the studied spatial extent than what we expected.

Our results proved that the overland distance is just as good predictor of metacommunity structure as the watercourse distance measures, resulting from the good dispersal capacity of macroinvertebrates via animal vectors. Thus, despite our prediction that AqPa species prefer stream corridors for dispersal (e.g., Bilton et al., 2001; Petersen et al., 2004), they may also disperse efficiently via the landscape (Grönroos et al., 2013).

Terrestrial-passive dispersal mode group (TePa)

Our results supported the prediction that the spatial component was relevant in structuring the metacommunity patterns of TePa species in spring (Fig. 4). An alternative explanation for the observed significant spatial signal can be the mass effect, when local dynamics (environmental control) are overridden by high dispersal rate (Cottenie, 2005; Ng et al., 2009). Specimens of the AqPa group are capable to hang on the substrate or vegetation. However, younger and weaker specimens which appear largely in spring are more exposed to the drift by the flow (Bilton et al., 2001). In Hungary, floods are more common in spring; therefore, flood-related drift dispersal ensures constant supply of new colonizers to these sites. Considerable numbers of AqPa species can be transported by the water currents, and this source-sink dynamics enable them to exist at sites, normally considered marginal or outside of their environmental range. Another source of the spatial signal might be the spatially structured but unmeasured environmental variables (shared fraction, $[E + S]$) or a spatial location effect that may be associated with some regional processes, which, at the same time explains the variation in environmental variables (Grönroos et al., 2013). The high shared fraction $[E + S]$ (even higher than the pure spatial factor) supports this explanation.

Winged adults of TePa can track environmental changes, thus environmental filtering was clearly the most prominent mechanism shaping metacommunities in summer (Fig. 4). TePa species are occasionally able to disperse over large spatial distances in high abundance (Johnson, 1969; Bohonak & Jenkins, 2003), and such effects can weaken the role of spatial variables in their organization (Saito et al., 2015). However, the lack of spatial pattern for weak dispersers could also be related to their poor ability to colonize neighbour habitats, thus weakening the spatial signal (Phillipsen & Lytle, 2013; Phillipsen et al. 2015; Cañedo-Argüelles et al., 2015).

Overland and watercourse distance measures were equally poor descriptors of community structure in the TePa dispersal group. This finding is supported by other studies in which

clear differences were lacking between overland and watercourse distances (Landeiro et al., 2012). Variance partitioning, however, resulted low explained variation of factors, thus, it was practically impossible to draw clear conclusions about the mechanisms shaping metacommunity structure of TePa. This could be explained by the low number of species in this group, which might result in creating biological artefacts or misleading outcomes at the community level.

Terrestrial-active dispersal mode group (TeAc)

In contrast to our predictions, TeAc did show small but significant spatial structuring (Figs. 3, 4). This finding is in contrast with previous studies, which emphasized that species with high dispersal capabilities are only influenced by environmental control (Grönroos et al., 2013; Heino, 2013). Members of the TeAc group are typically larger in size and stronger fliers than other macroinvertebrates, so they are able to control their flight for travelling relatively large distances across the land (Rundle et al., 2007) to find environmentally suitable habitats (Vonesh et al., 2009; Heino, 2013). However, we are assuming that dispersal rates might be so high and continuous at our spatial extent that it masks the effects of pure environmental filtering on species distributions. Thus, species may also occur at less optimal habitats through the dispersal from sites with better environmental conditions (Shmida & Wilson, 1985; Pulliam, 1988; Leibold et al., 2004).

Results proved that the overland distance is slightly better predictor of metacommunity structure than the watercourse distance measures. Despite our prediction that TeAc species prefer only overland dispersal, they may also disperse along the water corridor to a great extent. This might be caused by the high inside variation of dispersal strategy in TeAc mode group.

Seasonal differences in the relative role of environmental control and spatial structuring

Although the seasonal samples were collected from two consecutive years, the within year changes in macroinvertebrate community used to be higher than the year by year changes (e.g., Robinson et al., 2000; Brown et al., 2006; Mykrä et al., 2008), thus the seasonal comparison of the relative role of environmental and spatial control is valid by all means.

Our results supported the prediction that there were no seasonal differences in structuring processes on AqPa metacommunity (Fig. 4). The reason for this is that the AqPa species do not change their self-generated dispersal capacity throughout the year and that there were no seasonal differences in the species compositions (Table 2). These results are in agreement

with Sarremejane et al. (2017) who found temporally stable assembly mechanisms in a Mediterranean perennial river metacommunity.

Our results supported the prediction that there will be seasonal differences in the relative role of structuring processes in metacommunity dynamics of the TePa group (Fig. 4). Independently of the distance measure, spatial control is expressed in spring, and the metacommunity was under increasing environmental control in summer without spatial signal.

The seasonal changes in the relative role of spatial and environmental factors in TeAc group were observed only using watercourse distance measures; the environmental filtering in spring was completed a small spatial factor in summer and the seasonal changes in metacommunity pattern is considerable. Using overland distance measures, however, there was only a small seasonal difference in the total explained variance, thus the seasonal variation was not proved (Fig. 4). Dispersal traits have fundamental importance in metacommunity structuring (Heino et al., 2017). By dispersal proxies, only a coarse classification can be achieved, actual dispersal traits can be more intricate in nature. The disadvantage of the coarse classification is the most pronounced in the group with too much within-group seasonal variation, which can possibly hinder the detection of real metacommunity drivers in nature. The three-way (TeAc, TePa and TeAc) categorization addresses only one dimension of the dispersal strategy of species; however, they also disperse in time along different rates, and this influences the relative contribution of environmental and spatial factors in metacommunity structuring. For example, Odonata and Trichoptera have traditionally been characterized as “spring” and “summer” species, and have synchronized emergence. Aquatic Coleoptera and Heteroptera species, in contrast to dragonflies, do not only fly in the period after emergence but also do not disperse continuously. Apart from shorter flying periods, these insects stay in the water during most of their lifetime (usually up to 2 years). Moreover, the flight of many common species can be observed throughout the year in various numbers of individuals (Boda & Csabai, 2013). However, there are completely flightless taxa, either obligatory (e.g., Elmidae) or optional (e.g., Aphelocheiridae, Mesoveliidae), which cannot fly from the water but can reach long distances by swimming or walking (Boersma & Lytle, 2014). TePa would be a consistent group considering only the emergence period; however, the high generation times and the abundance of the species can make this group more diverse. The most consistent group is the AqPa, as they have both low within-group variation and low seasonal changes in their dispersal capacity. Using a classification method with more dimensions of dispersal (e.g.,

oviposition behaviour, life cycle length, generation time per year, wing size or time of emergence), we could most likely get new insights into the importance of dispersal on metacommunity structuring (Heino & Peckarsky, 2014; Tonkin et al., 2017).

Conclusion

Environmental control and spatial structuring are the most common processes, which regulate local community structure within a metacommunity. We found that all dispersal groups were influenced mainly by environmental factors in both seasons along with various additional impacts of the spatial components. Our findings suggest that metacommunities of taxa with temporally stable dispersal capacity (AqPa) have seasonally stable structuring processes, while the relative importance of structuring factors can vary seasonally in groups with seasonally changing dispersal capacity (TePa). These results further emphasize the use of dispersal traits in metacommunity research for a better understanding of the relative roles of environmental and spatial processes.

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References

- Allan, J. D. & M. M. Castillo, 2007. Stream ecology—structure and function of running waters. Springer, Dordrecht.
- Anderson, M. J., 2001. A new method for non-parametric multivariate analysis of variance. *Australian Ecology* 26: 32–46.
- AQEM Consortium, 2002. Manual for the application of the AQEM method. A comprehensive method to assess European streams using benthic macroinvertebrates, developed for the purpose of the Water Framework Directive. Version 1.0.
- Astorga, A., J. Oksanen, M. Luoto, J. Soininen, R. Virtanen & T. Muotka, 2012. Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography* 21: 365–375.

- Bilton, D. T., J. R. Freeland & B. Okamura, 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology, Evolution, and Systematics* 32: 159–181.
- Boda, P. & Z. Csabai, 2013. When do beetles and bugs fly? A unified scheme for describing seasonal flight behaviour of highly dispersing primary aquatic insects. *Hydrobiologia* 703: 133–147.
- Boersma, K. S. & D. A. Lytle, 2014. Overland dispersal and drought-escape behavior in a flightless aquatic insect, *Abedus herberti* (Hemiptera: Belostomatidae). *South-western Naturalist* 59: 301–302.
- Bohonak, A. J. & D. G. Jenkins, 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6: 783–796.
- Braak, C. J. F. T. & P. Smilauer, 2012. *Canoco Reference Manual and User's Guide: Software for Ordination (Version 5.0)*. Microcomputer Power, Ithaca.
- Brown, L. E., A. M. Milner & D. M. Hannah, 2006. Stability and persistence of alpine stream macroinvertebrate communities and the role of physicochemical habitat variables. *Hydrobiologia* 560: 159–173.
- Brown, B. L. & C. M. Swan, 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology* 79: 571–580.
- Cañedo-Argüelles, M., K. S. Boersma, M. T. Bogan, J. D. Olden, I. Phillipsen, T. A. Schriever & D. A. Lytle, 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Bio- geography* 42: 778–790.
- Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* 8: 1175–1182.
- Csabai, Z., Z. Kálmán, I. Szivák & P. Boda, 2012. Diel flight behaviour and dispersal patterns of aquatic Coleoptera and Heteroptera species with special emphasis on the importance of seasons. *Naturwissenschaften* 99: 751–765.
- De Bie, T., L. De Meester, L. Brendonck, K. Martens, B. Goddeeris, D. Ercken, H. Hampel, L. Denys, L. Vanhecke, K. Van der Gucht, J. Van Wichelen, W. Vyverman & S. A. J. Declerck, 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters* 15: 740–747.
- Dray, S., 2013. *Spacemaker: Spatial modelling*. R package version 0.0-5/r113. <https://R-Forge.R-project.org/projects/sedar/>
- Dray, S., P. Legendre & P. R. Peres-Neto, 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.

- Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, R. Bivand, F. G. Blanchet, M. De Cáceres, A.-B. Dufour, E. Heegaard, T. Jombart, F. Munoz, J. Oksanen, J. Thioulouse & H. H. Wagner, 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82: 257–275.
- Erős, T., P. Sály, P. Takács, A. Specziár & P. Bíró, 2012. Temporal variability in the spatial and environmental determinants of functional metacommunity organization— stream fish in a human modified landscape. *Freshwater Biology* 57: 1914–1928.
- Erős, T., P. Takács, A. Specziár, D. Schmera & P. Sály, 2017. Effect of landscape context on fish metacommunity structuring in stream networks. *Freshwater Biology* 62: 215–228.
- Fernandes, I. M., R. Henriques-Silva, J. Penha, J. Zuanon & P. R. Peres-Neto, 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37: 464–475.
- Göthe, E., D. G. Angeler & L. Sandin, 2013. Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology* 82: 449–458.
- Griffith, D. A. & P. R. Peres-Neto, 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87: 2603–2613.
- Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen & L. M. Bini, 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type and regional environmental context. *Ecology and Evolution* 3: 4473–4487.
- Heino, J., 2013. Environmental heterogeneity, dispersal mode and co-occurrence in stream macroinvertebrates. *Ecology and Evolution* 3: 344–355.
- Heino, J. & J. Alahuhta, 2015. Elements of regional beetle faunas: faunal variation and compositional breakpoints along climate, land cover and geographical gradients. *Journal of Animal Ecology* 84: 427–441.
- Heino, J. & H. Mykka, 2008. Control of stream insects assemblages: roles of spatial configuration and local environmental variables. *Ecological Entomology* 33: 614–622.
- Heino, J. & B. L. Peckarsky, 2014. Integrating behavioral, population and large-scale approaches for understanding stream insect communities. *Current Opinion in Insect Science* 2: 7–13.
- Heino, J., M. Grönroos, J. Soininen, R. Virtanen & T. Muotka, 2012. Context dependency and metacommunity structuring in boreal headwater streams. *Oikos* 121: 537–544.
- Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko & L.

- M. Bini, 2015a. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845–869.
- Heino, J., T. Nokela, J. Soininen, M. Tolkkinen, L. Virtanen & R. Virtanen, 2015b. Elements of metacommunity structure and community–environment relationships in stream organisms. *Freshwater Biology* 60: 973–988.
- Heino, J., J. Alahuhta, T. Ala-Hulkko, H. Antikainen, L. M. Bini, N. Bonada, T. Datry, T. Erős, J. Hjort, O. Kotavaara, A. S. Melo & J. Soininen, 2017. Integrating dispersal proxies in ecological and environmental research in the freshwater realm. *Environmental Reviews* 25: 334–349.
- Hering, D., A. Buffagni, O. Moog, L. Sandin, M. Sommerhäuser, I. Stubauer, C. Feld, R. Johnson, P. Pinto, N. Skoulikidis, P. Verdonshot & S. Zahrádková, 2003. The development of a system to assess the ecological quality of streams based on macroinvertebrates—design of the sampling programme within the AQEM project. *International Review of Hydrobiology* 88: 345–361.
- Holyoak, M., M. A. Leibold & R. D. Holt, 2005. *Metacommunities: spatial dynamics and ecological communities*, 1st ed. University of Chicago Press, Chicago.
- Johnson, C. G., 1969. *Migration and dispersal of insects by flight*. Methuen and Co Ltd., London.
- Kärnä, O. M., M. Grönroos, H. Antikainen, J. Hjort, J. Ilmonen, L. Paasivirta & J. Heino, 2015. Inferring the effects of potential dispersal routes on the metacommunity structure of stream insects: As the crow flies, as the fish swims or as the fox runs? *Journal of Animal Ecology* 84: 1342–1353.
- Landeiro, V. L., L. M. Bini, A. S. Melo, A. M. O. Pes & W. E. Magnusson, 2012. The roles of dispersal limitation and environmental conditions in controlling caddisfly (Trichoptera) assemblages. *Freshwater Biology* 57: 1554–1564.
- Legendre, P. & E. D. Gallagher, 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.
- Legendre, P., D. Borcard & P. R. Peres-Neto, 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monograph* 75: 435–450.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau & A. Gonzalez, 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

- Logue, J. B., N. Mouquet, H. Peter & H. Hillebrand, 2011. Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution* 26: 482–491.
- MET1, 2018. https://www.met.hu/eghajlat/magyarorszag_eghajlata/eghajlati_visszatekinto/elmult_evek_idojarasa/
- MET2, 2018. https://www.met.hu/eghajlat/magyarorszag_eghajlata/altalanos_eghajlati_jellemzes/sugarzas/
- MET3, 2018. https://www.met.hu/eghajlat/magyarorszag_eghajlata/eghajlati_visszatekinto/elmult_evszakok_idojarasa/
- Mezősi, G., 2016. *The Physical Geography of Hungary*. Springer, Switzerland.
- Mykrä, H., J. Heino & T. Muotka, 2008. Concordance of stream macroinvertebrate assemblage classifications: How general are patterns from single-year surveys? *Biological Conservation* 141: 1218–1223.
- Ng, I. S. Y., C. M. Carr & K. Cottenie, 2009. Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619: 133–143.
- Oksanen, J., R. Kindt, P. Legendre, B. O'Hara & M. H. H. Stevens, 2007. The vegan package. *Community ecology package* 10.
- Petersen, I., Z. Masters, A. G. Hildrew & S. J. Ormerod, 2004. Dispersal of adult aquatic insects in catchments of different land use. *Journal of Applied Ecology* 32: 934–950.
- Phillipsen, I. C. & D. A. Lytle, 2013. Aquatic insects in a sea of desert: population genetic structure is shaped by limited dispersal in a naturally fragmented landscape. *Ecography* 36: 731–743.
- Phillipsen, I. C., E. H. Kirk, M. T. Bogan, M. C. Mims, J. D. Olden & D. A. Lytle, 2015. Dispersal ability and habitat requirements determine landscape-level genetic patterns in desert aquatic insects. *Molecular Ecology* 24: 54–69.
- Plenzler, M. A. & H. J. Michaels, 2015. Terrestrial habitat quality impacts macroinvertebrate diversity in temporary wetlands. *Wetlands* 35: 1093–1103.
- Pulliam, H. R., 1988. Sources, sinks, and population regulation. *The American Naturalist* 132: 652–661.
- Quantum GIS Development Team, 2010. Quantum GIS Geographic Information System. <http://www.qgis.org>.
- R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

- Razeng, E., A. Morán-Ordóñez, J. B. Box, R. Thompson, J. Davis & P. Sunnucks, 2016. A potential role for overland dispersal in shaping aquatic invertebrate communities in arid regions. *Freshwater Biology* 61: 745–757.
- Robinson, C. T., G. W. Minshall & T. V. Royer, 2000. Interannual patterns in macroinvertebrate communities of wilderness streams in Idaho, USA. *Hydrobiologia* 421: 187–198.
- Rundle, S. D., D. T. Bilton & A. Foggo, 2007. By Wind, Wings or Water: Body Size, Dispersal and Range Size in Aquatic Invertebrates. In Hildrew, A. G., D. G. Raffaelli & R. Edmonds (eds), *Body Size: The Structure and Function of Aquatic Ecosystems*. Cambridge University Press, Cambridge: 186–209.
- Saito, V. S., J. Soininen, A. A. Fonseca-Gessner & T. Siqueira, 2015. Dispersal traits drive the phylogenetic distance decay of similarity in Neotropical stream metacommunities. *Journal of Biogeography* 42: 2101–2111.
- Sály, P. & T. Erős, 2016. Effect of field sampling design on variation partitioning in a dendritic stream network. *Ecological Complexity* 28: 187–199.
- Sarremejane, R., M. Cañedo-Argüelles, N. Prat, H. Mykrä, T. Muotka & N. Bonada, 2017. Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography* 44: 2752–2763.
- Schmera, D., D. Árvai, P. Boda, E. Bódis, Á. Bolgovics, G. Borics, A. Cserecsa, C. S. Deák, Á. E. Krasznai, B. A. Lukács, P. Mauchart, A. Móra, P. Sály, A. Specziár, K. Süveges, I. Szivák, P. Takács, M. Tóth, G. Várbíró, E. A. Vojtkó & T. Erős, 2018. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshwater Biology* 63: 74–85.
- Shmida, A. & M. W. Wilson, 1985. Biological determinants of species diversity. *Journal of Biogeography* 12: 1–20.
- Tolonen, K. T., Y. Cai, A. Vilmi, S. M. Karjalainen, T. Sutela & J. Heino, 2018. Environmental filtering and spatial effects on metacommunity organisation differ among littoral macroinvertebrate groups deconstructed by biological traits. *Aquatic Ecology* 52: 119–131.
- Tonkin, J. D., F. Altermatt, S. D. Finn, J. Heino, J. D. Olden, S. U. Pauls & D. Lytle, 2017. The role of dispersal in river network metacommunities: patterns, processes, and pathways. *Freshwater Biology* 63: 141–163.

- Trájer, A., T. Hammer, I. Kacsala, B. Tánzos, N. Bagi & J. Padisák, 2017. Decoupling of active and passive reasons for the invasion dynamics of *Aedes albopictus* Skuse (Diptera: Culicidae): comparisons of dispersal history in the Apennine and Florida peninsulas. *Journal of Vector Ecology* 42: 1–10.
- Van Leeuwen, C. H. A., G. Van der Velde, B. Van Lith & M. Klaassen, 2012. Experimental quantification of long distance dispersal potential of aquatic snails in the gut of migratory birds. *PloS ONE* 7: e32292.
- Vonesh, J. R., J. M. Kraus, J. S. Rosenberg & J. M. Chase, 2009. Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. *Oikos* 118: 1219–1229.
- Winegardner, A. K., B. K. Jones, I. S. Y. Ng, T. Siqueira & K. Cottenie, 2012. The terminology of metacommunity ecology. *Trends in Ecology and Evolution* 27: 253–254.

Figures and tables

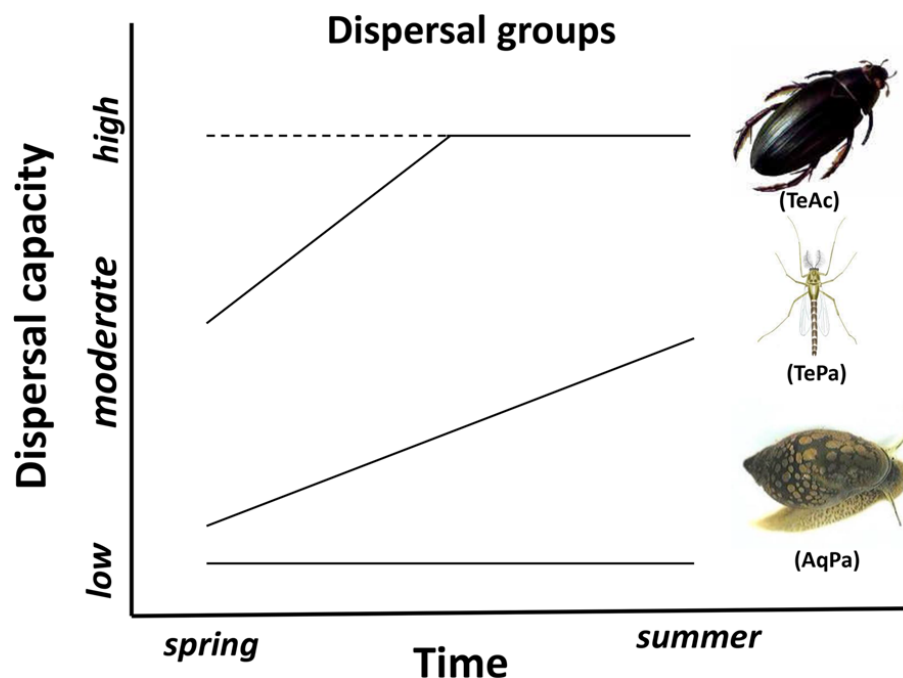


Fig. 1 Expected changes in dispersal capacity over time of three dispersal mode groups based on the literature data. Dotted line refers to an alternative option

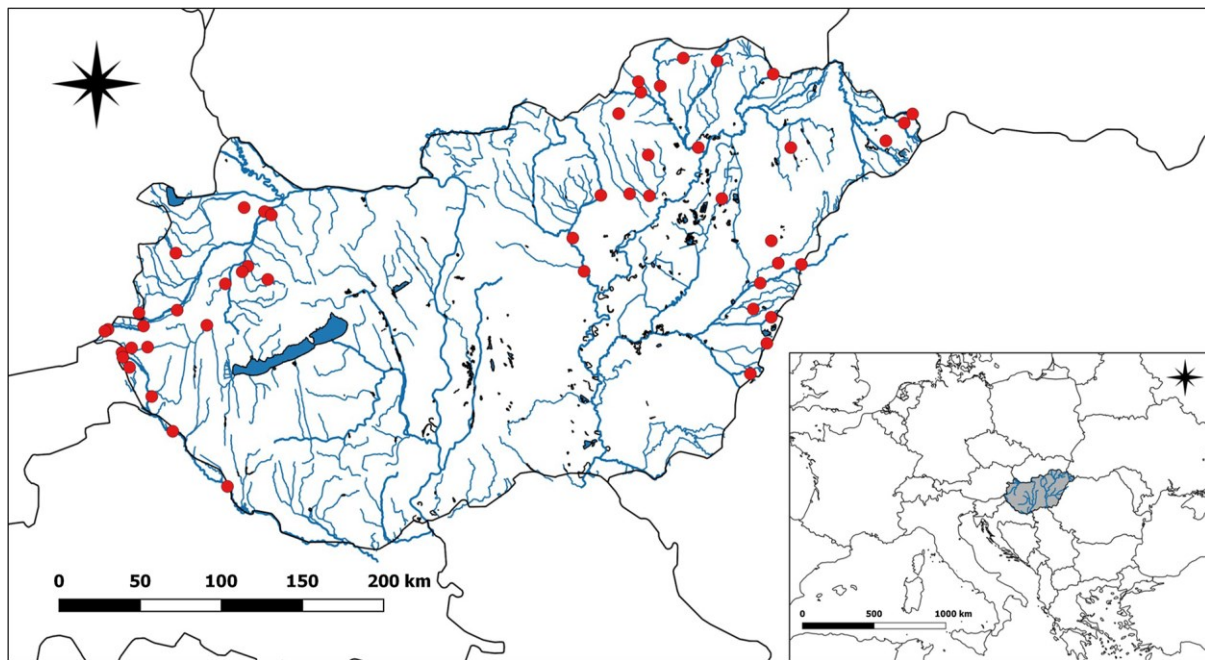


Fig. 2 Map of the study area with approximate positions of the sampling sites

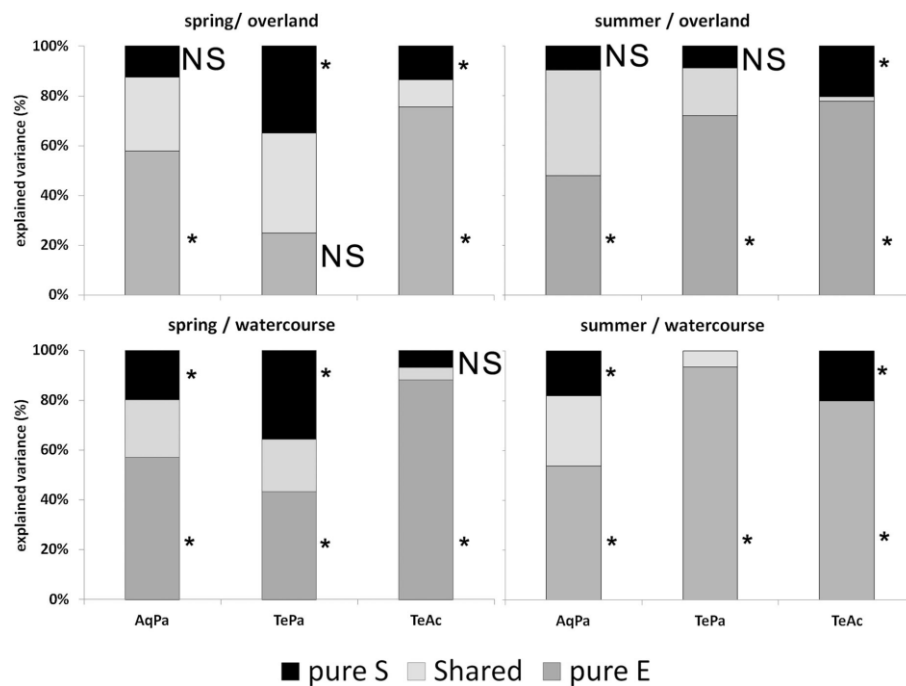


Fig. 3 Variation partitioning (%) of the macroinvertebrate dispersal mode groups decomposed by dispersal routes (watercourse–overland) and seasons (summer–spring). Three different components are given: pure environmental variation, pure spatial variation and the spatial structure in the species data that are shared by the environmental data (the unexplained variation was shown in Electronic Supporting Material Table 1). Significant results ($P < 0.05$) are indicated with *
















OVERLAND		DISPERSAL MODE GROUPS	WATERCOURSE	
SPRING	SUMMER		SPRING	SUMMER
				
				
				

Fig. 4 Significant ($P < 0.05$) pure environmental [E], spatial [S] and shared [E + S] fractions, when using overland distances (left) and watercourse distances (right)

Table 1 Comparison of environmental variables (mean \pm SE) between sampling sites

Variable	Total
Water chemistry	
Water temperature ($^{\circ}\text{C}$)	18.04 ± 0.52
pH	7.65 ± 0.1
O_2 (mg l^{-1})	8.6 ± 0.23
Conductivity ($\mu\text{S cm}^{-1}$)	639 ± 33
$\text{NO}_2^{-}\text{-N}$ ($\mu\text{g l}^{-1}$)	48.91 ± 3.75
$\text{NH}_4^{+}\text{-N}$ (mg l^{-1})	6.48 ± 1.61
P ($\mu\text{g l}^{-1}$)	175.14 ± 4.74
$\text{PO}_4^{3-}\text{-P}$ (mg l^{-1})	1.08 ± 0.09
Microhabitat, streambed morphology and hydrological features	
Megalithal and natural macrolithal > 20–40 cm (%)	2.06 ± 0.94
Artificial macrolithal > 20–40 cm (%)	0.54 ± 0.26
Mesolithal > 6–20 cm (%)	11.57 ± 2.04
Microolithal > 2–6 cm (%)	19.41 ± 2.56
Akal > 2 mm–2 cm (%)	18.28 ± 2.21
Psammal > 6 μm –2 mm (%)	18.14 ± 2.03
Argyllal < 6 μm (%)	30 ± 3.59
Submerged macrophytes (%)	5.44 ± 1.32
Emergent macrophytes (%)	16.76 ± 2.46
Living parts of terrestrial plants (%)	4.12 ± 0.49
Xylal (wood) (%)	3.04 ± 0.44
CPOM (deposits of coarse particulate organic matter) (%)	2.06 ± 0.79
FPOM (deposits of fine particulate organic matter) (%)	4.26 ± 1.32
Wetted width (m)	17.00 ± 2.56
Depth (cm)	60.47 ± 4.68
Current velocity (cm/s)	28.30 ± 2.31
Catchment	
Altitude (m)	145.02 ± 4.81
Water catchment size (km^2)	2732 ± 881.81
Land-use index	1.32 ± 0.04
Urban area (%)	5.77 ± 0.58
Natural area (%)	36.18 ± 1.84
Intensive agricultural area (%)	51.18 ± 1.94
Non-intensive agricultural area (%)	6.86 ± 0.82

Table 2 Results of ADONIS for the whole macroinvertebrate community and the three dispersal mode groups separately in relation to seasons

Source of variance	df	F	R ²	p
Total				
Season	1	3.1547	0.03126	0.0256*
Residuals	96		0.95122	
Dispersal groups				
AqPa				
Season	1	0.4993	0.00426	0.8579
Residuals	95		0.80989	
TePa				
Season	1	4.3984	0.04360	0.0001***
Residuals	92		0.91190	
TeAc				
Season	1	4.6607	0.04360	0.0001***
Residuals	96		0.89797	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3 Summary statistics of distance–decay relationships (adjusted R²) in different dispersal model groups for both distances and in both seasons

Relationship	Distance	Season	AqPa R ²	TePa R ²	TeAc R ²
Distance–decay	Overland	Spring	NS	0.0105***	NS
		Summer	0.0043*	NS	0.0061**
	Watercourse	Spring	0.0059**	0.0120***	0.0051*
		Summer	0.0072**	NS	0.0131***
Relationship		Season	AqPa R ²	TePa R ²	TeAc R ²
Environment × Community		Spring	0.1086***	NS	0.0942***
		Summer	0.0850***	0.0101***	0.1364***

NS no significant relationship * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 4 Results of the Mantel tests among Bray–Curtis community distance among sites versus overland and watercourse distances in both seasons

Season	Distance	AqPa r	TePa r	TeAc r
Spring	Overland	0.11**	0.12**	NS
	Watercourse	0.08*	0.11**	NS
Summer	Overland	0.11**	NS	0.13**
	Watercourse	0.10**	NS	0.12**

The table includes Mantel statistic r and significance levels

NS non-significant

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$