The role of dispersal mode and habitat specialisation in metacommunity structuring of aquatic macroinvertebrates in isolated spring fens

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SUMMARY
1. The relevance of environmental and spatial processes for species distributions varies among environments and types of metacommunities. Here, for the first time, we use modern statistical approaches to test the contribution of these two processes in structuring ecologically unique and threatened biotas of insular spring fens. We applied two species categorisations, common/rare and generalists/specialists, to disentangle the roles of dispersal capacity and habitat specialisation.
2. In accordance with current understanding of headwater ecosystems, we found that environmental processes played a major role in most of the spring fen taxonomic and functional groups. However, we observed significant spatial structure in passive dispersers (Clitellata, a class of annelid worms), common species and habitat specialists.
3. Spatial processes played the leading role in structuring the metacommunity of passively dispersing specialists. In contrast, all analysed insect groups, even those known to be poor dispersers, were able to reach virtually all favourable sites.
4. We conclude that dispersal mode (active versus passive) and, to a lesser extent, habitat specialisation are the main factors determining the mechanism of spring fen metacommunity structuring.

Keywords: dispersal, habitat specialisation, macroinvertebrates, metacommunity structuring, spring fens

Introduction
During the past decade, ecologists have devoted increasing attention to the relative importance of processes driving the composition of metacommunities (Leibold et al., 2004; Cottenie, 2005; Gravel et al., 2006; Dray et al., 2012). Communities composed of species that occupy different environmental niches are expected to be structured mostly by habitat features that create various environmental filters (species sorting; Chase & Leibold, 2003; Leibold et al., 2004). However, in communities of ecologically equivalent species, distributions and community structure are strongly influenced by the dispersal capacity of each species (neutral model; Hubbell, 2001). The relative importance of dispersal (spatial processes) and species sorting (environmental processes) has been found to vary among different types of metacommunities and at different spatial scales (Fenchel & Finlay, 2004; Cottenie, 2005; Hájek et al., 2011; De Bie et al., 2012; Grönroos et al., 2013). Thus, systematic differences have been repeatedly found between microorganisms and macroorganisms, taxa with microscopic and macroscopic propagules, passive and active dispersers, and tropical and extratropical metacommunities.

A marked difference has also been observed between lentic and lotic systems, although dispersal mode has been recognised as a key trait determining assembly structure in both environments (De Bie et al., 2012; Grönroos et al., 2013). Lotic communities usually show a weaker imprint of dispersal constraints than lentic communities, due to the linear or dendritic network connectivity of the former (Heino & Mykrä, 2008; Shurin, Cottenie & Hillebrand, 2009; De Bie et al., 2012; Grönroos et al., 2013). There is also a growing body of
evidence that macroinvertebrate communities in headwater lotic systems are structured mainly by environmental filtering, as demonstrated for headwater streams (Brown & Swan, 2010; Siqueira et al., 2012; Grönroos et al., 2013). However, to date, no study has addressed metacommunity structuring in spring fen habitats, which are characterised by specific environmental conditions that make them distinct from all other habitats in riverine systems, including headwater streams. Spring fens are wetlands fed by ground water, which host a characteristic vegetation (Hájek et al., 2006). They form isolated patches, although they may be connected via a stream network. Spring fens are not affected by extreme hydrological events (floods or droughts) and fluctuations in water chemistry are limited, although dependent on vegetation type (Hájková, Wolf & Hájek, 2004). This implies a high level of environmental stability, which may strengthen the relative role of spatial processes, because spring fen species may be less likely to need to disperse, compared with those living in unstable, fluctuating environments.

Based on their environmental distinctness and the isolation of spring fen assemblages from the regional species pool, we would predict, particularly for spring fen specialists, a possible role for net flows of individuals created by differences in population sizes in different patches negligible (mass effect; Chase et al., 2005). As spring fens belong to the headwater zone of streams, we might expect spring metacommunities to be structured primarily by environmental filtering, as suggested by Brown & Swan (2010) for headwaters in general. However, as spring fens are mostly rare habitats, usually of small area and situated apart from each other, we cannot a priori exclude a role for spatial constraints in shaping their communities. In particular, taxa with low dispersal abilities and strong associations with these specific habitats are likely to exhibit significant spatial patterns. As the studied spring fens also vary in their origin, mostly during the Holocene (Hájková et al., 2012), modern distributions of species may reflect, for example, a migration from paleorefugia to more recently formed patches (Nekola, 1999; Horsák et al., 2012).

In this study, we explore whether the pattern of metacommunity structuring observed in headwaters (Heino & Mykrä, 2008; Brown & Swan, 2010) also occurs in spring metacommunities. Specifically, we tested whether the structure of macroinvertebrate metacommunities in isolated spring fen habitats, distributed along a sharp environmental gradient, shows evidence of dispersal constraints at both the broad and fine spatial scales. We hypothesised that if any significant effect of a pure spatial fraction is evident, it should be related to dispersal mode and the ability of taxa to disperse. Thus, we expected a higher fraction of pure spatial effect for passively dispersed aquatic Clitellata (a class of annelid worm) than insects with winged adults (Trichoptera, Plecoptera and Ephemeroptera combined, and Chironomidae). Clitellata are permanent residents of spring habitats and have a relatively low ability to disperse among spring fen sites; zoochory is their most important dispersal mechanism (Boileau & Hebert, 1991; Terhivuo & Saura, 2006). All the studied insect groups have terrestrial adults that are capable of flight, but nevertheless, they differ in dispersal abilities. Thus, a systematic difference in the ability to reach suitable sites can be expected. Plecoptera and Ephemeroptera are known to be weaker dispersers than most other aquatic insects (Yasick, Krebs & Wolin, 2007). Trichoptera communities in the spring fens combine large species with very good dispersal abilities and small species with relatively low dispersal abilities (Sode & Wiberg-Larsen, 1993), resulting in an intermediate level of dispersal for the whole group. Although Chironomidae are moderate active dispersers (Delettre, Tréhen & Grootaert, 1992), their main means of dispersal over large distances is passive transport of swarming individuals by wind (Johnson, 1969). Since this means of transport is relatively frequent and very effective (Paz & Broza, 2007), we consider Chironomidae to be very good dispersers.

Dispersal abilities may also differ among assemblages defined by commonness/rarity and habitat specialisation. The role of environmental and spatial processes for common and rare species (Siqueira et al., 2012) or habitat specialists and generalists (Pandit, Kolasa & Cottenie, 2009) remains poorly explored. Siqueira et al. (2012) hypothesised that common species should be mainly structured by environmental factors and rare species by dispersal limitation. They found that environmental processes exclusively structured both common and rare species assemblages in Brazilian streams. However, different conclusions may be expected if species are categorised according to their habitat specialisation, because not all common species are necessarily generalists and not all specialists are necessarily rare. While specialists should respond mainly to habitat features, generalists are expected to be more restricted by spatial processes. In our study system, we can define habitat specialisation using a colonisation dynamic pattern based on species–habitat association (Watson, 2002). Whittaker (1998) termed habitat specialists as ‘interpatch dispersers’, and generalist species originating from the surrounding matrix as ‘matrix-derived’ species. Thus, species that are
tightly associated with spring fen environments (habitat specialists) may find it difficult to colonise environmentally suitable patches (Horsák et al., 2012). Such species are confined to particular habitat(s) in the landscape, although they can be abundant in these communities. In contrast, species that also occupy other habitats can more readily reach a target spring fen from the surrounding matrix, using other aquatic habitats as stepping stones to spread among isolated fens. Using this concept, combined with the hypothesis proposed by Siqueira et al. (2012), the pure spatial fraction should be higher for habitat specialists (i.e. species rare in the landscape) than for generalist species, which ought to be common in the landscape. Furthermore, the spatial signal should become stronger with a decreasing ability to disperse.

Our main goal was to provide the first evidence about the role of environmental and spatial processes in structuring aquatic invertebrate assemblages in isolated spring fens. We classified our metacommunities not only taxonomically, but also based on species commonness/rarity and habitat specialisation. We assumed a prevalent role for environmental processes, because strong ecological gradients exist in spring fens and because the fens represent a distinct part of headwater systems. However, we also expected an important degree of spatial structuring in taxa with low dispersal abilities (e.g. passive dispersers and habitat specialists). Our hypotheses are based on three main assumptions: (i) spring fen specialists are unable to occupy surrounding aquatic habitats, hampering dispersal among isolated spring fen patches with favourable conditions, (ii) dispersal of passive dispersers depends on appropriate vectors and (iii) populations of common species can be maintained by a constant immigration of specimens from the surrounding landscape (mass effect).

**Methods**

We aimed to reduce limitations that can hamper inference about processes shaping assemblages in spring fens. First, data on taxonomic and functional groups were collected from the same well-defined sampling plots under a standardised sampling protocol. Second, key environmental factors for spring fen macroinvertebrates were measured at each location. Because climatic and local factors are often spatially structured, the resulting pure effect of spatial variables is frequently overestimated due to the difficulty of establishing a set of the most relevant environmental filters (Dray et al., 2012; Chang et al., 2013). Thus, we designed our sampling along a sharp environmental gradient of water mineral richness (which plays the main role in structuring spring fen communities; Hájek et al., 2006), ranging from mineral-rich calcareous fens to mineral-poor, acidic Sphagnum fens. As mineral content is closely related to substratum characteristics (mainly grain-size composition and organic carbon content), which play an important role in our system as well (Omelková et al., 2013), we can precisely describe the main environmental predictors of the studied communities. Furthermore, a possible overestimation of the spatial component on a large scale was controlled by involving climatic variables in the analysis, as these are often strongly spatially structured (Currie et al., 2004).

Fifty-nine isolated spring fen sites in the Western Carpathians (Fig. 1) were selected along the entire gradient of mineral richness. Two main mesohabitats, differing mainly in flow conditions (standing and flowing water), were sampled at each site in spring (March–April) and autumn (August–September). Altogether, 236 quantitative samples (one per mesohabitat and season, four in total per site) were taken using a hand net (mesh size 500 μm) from a quadrat defined by a metal frame (25 × 25 cm²) to a depth of 5 cm. Samples were manually sorted under a dissecting microscope, and specimens were identified to the lowest possible taxonomic level (species in most cases) using available identification literature and the authors’ comparative collections originating from previous sampling and collection of adults. A set of 35 environmental variables were measured and explored using PCA biplots (function ‘cleanplot.pca’, Borcard et al., 2004). Based on Spearman correlations (critical value of rho = 0.70) and the ecological relevance of each factor for the studied organisms, a subset of 18 relevant variables was selected for dbRDA analysis: pH, water conductivity, water temperature, discharge, the amount of dissolved oxygen, the concentration of important chemical ions (Ca²⁺ and Mg²⁺, Na⁺ and K⁺, Fe³⁻, NO₃⁻, PO₄³⁻, SO₄²⁻), the amount of organic and inorganic substratum, total organic carbon (TOC), cover of vascular plants, Ellenberg indicator values for moisture and temperature (for more details see Horsák et al., 2007), average annual air temperature and annual precipitation sum. Details of sample processing, measurements of the variables and a basic description of the study area and sites, along with a list of identification literature used, are provided in Appendix S1 in Supporting Information and also described by Omelková et al. (2013) and Rádková et al. (2014).

The three categorisations used in the analysis (Table 1) were as follows: (i) taxonomic (Clitellata, Ephemeroptera

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and Plecoptera combined, Trichoptera, and Chironomidae), (ii) functional (habitat specialists and matrix-derived generalists) and (iii) based on total abundance (rare versus common species). Specialists were defined as taxa that, within the studied region, are not expected to establish viable populations except in spring fen habitats (not in so-called stepping stone habitats), despite the fact that they may be known to occur in such habitats in remote areas (e.g. in lakes in boreal regions). For the identification of specialists, we searched available literature sources (Bitušík et al., 2000; Šporka, 2003; Vallenduuk & Moller Pillot, 2007; Graf et al., 2008, 2009; Moller Pillot, 2009, 2013; Zahrádková et al., 2009; Anderson, Cranston & Epler, 2013) and, in the case of missing data, we used available unpublished data. To distinguish between rare and common species, we used two approaches involving rank abundance curves (Magurran, 2004). First, rare and common species were determined by the inflexion point (the point at the curve where its direction sharply changes, Siqueira et al., 2012; see Figure S1). The resulting matrices, however, differed in the amount of information that they contained. Thus, accumulated information in each rank abundance curve was calculated as the cumulative sum across species of the binomial variance (for details, see Lennon et al., 2004, 2011). Each matrix of rare species was reduced by a stepwise removal of species with the lowest abundances until the same information content was obtained as for the respective matrix of common species. Functional and rare versus common species categorisations were used not only for the entire assemblage, but also within taxonomic groups and separately for passively and actively spreading taxa; this resulted in the analysis of 31 data subsets.

**Statistical analysis**

Species abundances in the four samples from each site were combined before the analysis. Abundance data were logarithmically transformed \[\log (x + 1)\], and 42 taxa found at a single site with an abundance of fewer than 10 specimens were excluded to remove the influence of dominant species and reduce noise, respectively. Two explanatory models for each invertebrate data matrix were constructed using distance-based RDA (Legendre & Anderson, 1999): an environmental model and a spatial model. Variables (both, environmental and spatial) entered into the model were selected by forward selection (Blanchet, Legendre & Bocard, 2008). Spatial variables were obtained by distance-based Moran’s eigenvector maps (dbMEMs, Dray, Legendre & Peres-Neto, 2006). The dbMEMs, formerly called PCNM eigenvectors (Principal Coordinates of Neighbour Matrices, Borcard et al., 2004), are based on simple geographical distances. Only dbMEMs with positive eigenvalues \([\text{Moran’s } I > E(I)]\) expressing positive spatial correlation were considered. Together, they represent the multiscale distance relationships among the sites. As dbMEM analysis insufficiently covers linear trends, all taxa data sets were tested for linear trends prior to dbMEM analy-
sis using geographical coordinates as explanatory variables in the dbRDA model. When linear trends were significant, the forward selection of MEM variables was performed using the detrended residuals of the response variables from the dbRDA model. A total of 15 dbMEMs resulted, and their spatial structure and scale were explored by trend-surface analysis, a regression model calibrated over the entire study area (Borcard, Gillet & Legendre, 2011) and by variograms (Bellier et al., 2007).

Three scales were identified: broad scale (V1–3 with wavelength of 50–70 km), intermediate scale (V4–13 with wavelength of 30–50 km) and fine scale (V14 and V15 with wavelength of 20–30 km).

When and only when both dbRDA models (environmental and spatial) for a given category (taxonomic, functional and rareness-related) were significant, was the total compositional variance of the appropriate category partitioned into the purely environmental fraction, purely spatial fraction, a fraction with spatially structured environmental variance and the unexplained variance. Significances of purely environmental and spatial fractions were tested by the 9999-permutation procedure, and an adjusted $R^2$ was computed as an unbiased estimate of the explained variance of the fractions (Peres-Neto et al., 2006).

All analyses were performed in R software (version 3.0.2, R Core Team, 2013) with the use of ‘vegan’ (Oksanen et al., 2011), ‘packfor’ (Dray, 2011), ‘PCNM’ (Legendre et al., 2012) and ‘spacemaker’ (Dray, 2010) packages.

### Results

**Environmental and spatial variables**

With few exceptions, total organic carbon (TOC) and the amount of dissolved oxygen were the most important environmental factors for almost all taxon groups regardless of their categorisation (Figs 2 & 3). Trichoptera were the only group that did not show a significant association with any of the three substratum parameters used, while rare Clitellata species composition responded to the amount of organic substratum only weakly. The amount of dissolved oxygen, closely linked to flow conditions, was not significant in the case of Ephemeroptera and Plecoptera combined or the matrix of common species (Fig. 2). Water temperature was strongly associated with common species, whether actively or passively dispersing, and also with passive specialists and active generalists. Water pH and cation content ($\text{Ca}^{2+}$, $\text{Mg}^{2+}$, $\text{Na}^+$, $\text{K}^+$), both of which relate to the mineral richness gradient, were the main predictors of compositional changes of permanent fauna, being particularly pronounced in passive specialists and rare species (Fig. 3). In contrast, taking all taxa together, generalists, specialists and common species responded only weakly to the gradient. Among actively spreading taxa, the water pH gradient was significantly reflected only by Trichoptera and Chironomidae assemblages and specialised species.

The spatial linear trend represented by longitude and latitude was significantly related to almost all analysed data sets (30), except for Ephemeroptera and Plecoptera specialists, for which neither the environmental nor the spatial model was significant (Figure S2). For two of the nine data sets with a significant pure spatial fraction, geographical coordinates were the only significant

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### Table 1 Numbers of species, sum of their frequencies and total abundances in each taxonomic category

<table>
<thead>
<tr>
<th>No. of analysed taxa</th>
<th>Sum of Freq.</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>All species</td>
<td>2247</td>
<td>69 035</td>
</tr>
<tr>
<td>Specialists</td>
<td>837</td>
<td>24 833</td>
</tr>
<tr>
<td>Generalists</td>
<td>1410</td>
<td>44 202</td>
</tr>
<tr>
<td>Common species</td>
<td>523</td>
<td>44 350</td>
</tr>
<tr>
<td>Rare species</td>
<td>1724</td>
<td>20 699</td>
</tr>
<tr>
<td>Rare species – reduced</td>
<td>488</td>
<td>13 007</td>
</tr>
<tr>
<td>Clitellata</td>
<td>626</td>
<td>24 116</td>
</tr>
<tr>
<td>Specialists</td>
<td>58</td>
<td>6449</td>
</tr>
<tr>
<td>Generalists</td>
<td>568</td>
<td>19 641</td>
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<tr>
<td>Common species</td>
<td>236</td>
<td>20 861</td>
</tr>
<tr>
<td>Rare species</td>
<td>390</td>
<td>5229</td>
</tr>
<tr>
<td>Rare species – reduced</td>
<td>211</td>
<td>3892</td>
</tr>
<tr>
<td>Insect taxa</td>
<td>1621</td>
<td>42 945</td>
</tr>
<tr>
<td>Specialists</td>
<td>779</td>
<td>18 384</td>
</tr>
<tr>
<td>Generalists</td>
<td>842</td>
<td>24 561</td>
</tr>
<tr>
<td>Common species</td>
<td>287</td>
<td>23 489</td>
</tr>
<tr>
<td>Rare species</td>
<td>1334</td>
<td>19 456</td>
</tr>
<tr>
<td>Rare species – reduced</td>
<td>185</td>
<td>8221</td>
</tr>
<tr>
<td>Ephemeroptera + Plecoptera</td>
<td>251</td>
<td>13 278</td>
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<tr>
<td>Specialists</td>
<td>71</td>
<td>1952</td>
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<tr>
<td>Generalists</td>
<td>180</td>
<td>11 326</td>
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<tr>
<td>Common species</td>
<td>136</td>
<td>12 160</td>
</tr>
<tr>
<td>Rare species</td>
<td>115</td>
<td>11 118</td>
</tr>
<tr>
<td>Rare species – reduced</td>
<td>59</td>
<td>868</td>
</tr>
<tr>
<td>Trichoptera</td>
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<td>4870</td>
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<tr>
<td>Specialists</td>
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<tr>
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<tr>
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<tr>
<td>Chironomidae</td>
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<td>12 464</td>
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<tr>
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<td>12 333</td>
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</tr>
<tr>
<td>Rare species – reduced</td>
<td>246</td>
<td>6419</td>
</tr>
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</table>
spatial variables (Figs 2, 3, S2 & S3). Additionally, dbMEMs representing broad-scale (V1–3), intermediate-scale (V4–13) and fine-scale (V14–15) distance relationships among the sites, were selected mainly for permanent fauna (all Clitellata) (V5 and V9, Fig. 2a), common passive species (V1, V5 and V9, Fig. 3a) and passive specialists (V1, V3, V5, V9 and V15, Fig. 3a). Furthermore, taking all taxa together, significant eigenvectors were found for generalists (V5 and V14, Fig. 2b) and common species (V5, V9 and V14, Fig. 2c), and also for active generalists (V5, Fig. 3b).

Relative importance of environmental and spatial variables

The vast majority of species composition variance could be explained by environmental factors in most of the analysed metacommunities (Figs 2 & 3). Clitellata, the group with only passive dispersal, were exceptional because their pure spatial component proved significant (Fig. 2a) and suggested both broad-scale and intermediate-scale structuring of their metacommunities. However, only the former (longitudinal pattern) could not also be explained by spatially structured environmental
heterogeneity. Assemblages of insects exhibited no significant purely spatial patterns at all, irrespective of how much they differed in dispersal ability.

A significant pure spatial pattern due to longitudinal structuring was found in the species composition of fen habitat specialists (all taxa combined), but not of generalists, although for the latter, there was a suggestion of structuring at all spatial scales (Fig. 2b). On the other hand, patterns in the proportions of explained variance were notably similar for specialists and generalists.

Contrasting patterns were observed between the variance partitioning of common and rare species. Common species were highly spatially structured, although most of this variance was shared with environmental variation (Fig. 2c). Conversely, variance in the rare species metacommunity was exclusively associated with environmental heterogeneity without any pure spatial fraction. The only possible influence of dispersal processes for rare species composition was observed at a broad scale (longitude, latitude), but this was fully explained by environmental variance and was insignificant. The pattern was the same for the matrix adjusted to include the same information content (for more details, see Figure S3a).

To explore whether combinations of two traits (dispersal mode and rarity or specialisation) can provide better insight into metacommunity structuring, we ran the same analysis for both passive and active dispersers divided into rare versus common species or generalist versus specialists (Fig. 3). Species composition of actively dispersing rare species and specialists was almost exclusively controlled by environmental processes in both cases (Fig. 3b). A slightly larger effect of spatial processes was observed in common species and
generalists with an active dispersal, but was significant only for the generalists. The patterns observed for generalists and rare species were essentially identical among passively and actively spreading taxa (Fig. 3a), and the patterns remained virtually unchanged for adjusted matrices of rare species (Figure S3a). In contrast to generalists and rare species, passively spreading habitat specialists and common species exhibited the highest pure spatial component, which included spatial patterns on all three spatial scales.

A unique pattern among all of the analysed metacommunities was observed for passively dispersing specialists (Fig. 3a). The pure spatial fraction explained the highest amount of variance of species composition in this case, while the contribution of the pure environmental fraction was very low and not significant. Nevertheless, only a broad-scale structuring of passively dispersing specialists could not be linked to environmental conditions.

**Discussion**

This is the first study to extend knowledge of metacommunity structuring of aquatic macroinvertebrates to spring fen habitats. Our results highlight a prevalent role for environmental processes in the composition of these assemblages. This accords with existing evidence from various headwater systems and other stream habitats (Heino & Mykrå, 2008; Brown & Swan, 2010; Heino \textit{et al.}, 2012; Siqueira \textit{et al.}, 2012). However, we observed several important differences from previous reports and these may have general importance because they indicate also a significant effect of dispersal constraints, the magnitude of which seems to be linked to dispersal mode and habitat specialisation.

**Active versus passive dispersers**

A leading role for environmental conditions in determining species composition in our system was obvious for both actively spreading (insects with flying adults) and passively dispersing (Clitellata) taxa. Assemblages in these fen habitats were controlled mainly by organic content of the substratum and by the amount of dissolved oxygen. Substratum characteristics and substratum stability are the most often reported environmental predictors of spring assemblages (Lindegaard \textit{et al.}, 1998; Ilmonen & Paasivirta, 2005), while the amount of dissolved oxygen mostly relates to the stability of the water regime (Rádková \textit{et al.}, 2014).

Although the role of environmental predictors showed a high consistency among the studied groups, obvious distinctions were observed for spatial variables. Only negligible relationships between spatial location and species composition were found for all groups of actively dispersing species, as previously reported from various geographical regions, including boreal (Heino & Mykrå, 2008; Grönnroos \textit{et al.}, 2013) and tropical zones (Landeiro \textit{et al.}, 2012). Thus, we did not observe any differences among the actively spreading taxa studied, despite the facts that some differences in their dispersal abilities can be presumed based on published data on dispersal capacities and that the studied sites were located in different catchments and/or separated by high mountain ranges. Grönnroos \textit{et al.} (2013) obtained similar results in three boreal stream networks at various spatial scales, suggesting a general pattern of prevalence of environmental sorting for actively dispersing taxa, regardless of the spatial extent studied. On the other hand, it needs to be born in mind that our results may have been confounded by within-group variation in dispersal abilities, which might differ among species of the same taxonomic group, as for our group of Plecoptera and Ephemeroptera combined. As there are very few studies of individual species’ dispersal abilities, particularly in the Chironomidae, it was impossible to precisely classify our studied species in order to obtain groups that were distinctly different in their dispersal capacity. Thus, the taxonomic approach was the only possibility for any finer categorisation of the insects.

In contrast, passively dispersing taxa showed a significant spatial signal, although most of this variation was autocorrelated with environmental variation and pure spatial structuring was found only at the broadest spatial scale. This may indicate a possible role of colonisation history at our study sites, whose Holocene origins vary markedly (Hájková \textit{et al.}, 2012). For passively dispersing species in particular, there may have been sufficient time to colonise nearby sites that originated a hundred years ago, but potentially longer may be required to reach remote and isolated sites, especially for habitat specialists (Hájek \textit{et al.}, 2011). It is important to note that only one group of passive dispersers was involved in this study, which makes extension of these findings difficult. Nevertheless, results obtained in an investigation of Mollusca and Ostracoda assemblages at spring fens in the same study area (Hájek \textit{et al.}, 2011; M. Zhai, O. Nováček & D. Výravský, unpublished data) support the results obtained for Clitellata. Passive and poor dispersers have repeatedly been found to exhibit strong spatial structuring of their populations, especially...
in insular systems such as lentic waters (Beisner et al., 2006; De Bie et al., 2012). This could, however, also be explained by their dependence on suitable vectors with little possibility of an active choice of suitable environments (Grönonroos et al., 2013).

It is apparent that all spatial processes related to dispersal limitation are closely associated with the spatial scale considered, and the importance of dispersal constraints can be expected to increase with increasing geographical range (Mykrä, Heino & Muotka, 2007; Heino et al., 2012). Heino & Mykrä (2008) found that different dispersal abilities did not affect community structure in a study of headwaters at a scale of about 60 km. Likewise, no spatial structuring of insect metacommunities was detected in streams along transects of 15 km (Landeiro et al., 2012), 60 km (Heino et al., 2012) or even 180 km (Grönonroos et al., 2013). In a disconnected system of low-altitude ponds, only a weak signature of dispersal limitation was found for insects within an area of 30 500 km² (De Bie et al., 2012). On the other hand, lower dispersal abilities of aquatic invertebrates contributed to significant spatial structuring in streams over a larger spatial scale of about 1100 km (Astorga et al., 2012). The same pattern has also been shown for highly isolated habitats, such as boreal lakes within an area of about 170 km² (Heino, 2013) and small rock pools distributed within only a 25-m radius (Pandit et al., 2009). This suggests that not only the size of the studied area, but also the scale of isolation and natural barriers are involved in the creation of spatial patterns. Our study extent can be regarded as intermediate or small (c. 200 km), although the study sites were isolated by various topographical barriers. However, dispersal mode only played a predominant role in structuring our assemblages when large categories (active versus passive) were considered.

Species commonness and habitat specialisation

Our results showed that processes affecting community composition can differ when considering species commonness and habitat specialisation. This suggests that dispersal abilities do not necessarily correspond to the taxonomic classification of organisms used in most previous studies (e.g. Hájek et al., 2011; Astorga et al., 2012; De Bie et al., 2012; Heino, 2013). Commonness and rarity is usually determined simply according to total abundances and/or frequencies of occurrences. Landeiro et al. (2012) assumed that the distribution of common species should be mainly related to environmental conditions because dispersal limitations were unlikely. In contrast, Siqueira et al. (2012) found a higher amount of variation was explained by a pure spatial fraction for common than for rare species in most cases when four stream macroinvertebrate data sets were examined. We have come to the same conclusion because common species from spring fens reflected a clear spatial structure at all spatial scales, with a significant contribution at the broadest scale. Common species in our spring fen samples included two contrasting types, the distribution of which may be controlled by two distinct mechanisms. The first type consists of generalist species with abundant populations, possibly maintained by constant immigration of specimens from the surrounding aquatic habitats (i.e. mass effect). The second type of common species includes clear habitat specialists, reaching high densities in the favourable conditions of specific habitats. Such habitat specialists may be limited by their narrow environmental niches, which restrict the colonisation of other aquatic habitats and also hamper their ability to find new habitat patches with suitable conditions. Both of these scenarios could lead to a greater importance of spatial processes in structuring common species assemblages, but individual species structuring can be detected at different spatial scales.

We assume that fine-scale structuring may influence common generalists due to a greater importance of mass effect (Brown & Swan, 2010), in contrast to specialists with abundant populations that are more likely to express significant spatial signals at broader scales. We also obtained the highest proportion of total explained variation for common species, which may be linked to a high probability of detecting species with high population densities. In contrast, rare species in all cases were significantly controlled only by the pure environmental fraction and spatially structured environmental conditions, and their total explained variation was mostly rather low. Rare species may be missing from some sites due to their high environmental sensitivity; furthermore, their generally low population densities make their detection at sites more difficult, potentially leading to higher noise in the data.

In contrast to the determination of species commonness and rarity, a classification of species along the generalist–specialist gradient is quite challenging for the majority of aquatic habitats. Relative niche widths, estimates of rarity or efficiency in reaching suitable habitats are among the most commonly used metrics for distinguishing habitat specialists and generalists (Pither & Aarssen, 2005; Fridley et al., 2007). However, such procedures tend to assume generalists are abundant and common species, in contrast to habitat specialists that are

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rare at local and regional scales, and thus miss those specialists that are able to achieve high population densities.

Very few studies have compared habitat specialists and generalists in aquatic systems from the perspective of metacommunity processes. Pandit et al. (2009) and Funk, Schiemer & Reckendorfer (2013) showed that the variation of invertebrate generalist communities from rock pools and Mollusca generalists from a lowland Danube floodplain, respectively, were more influenced by spatial processes, while specialists tightly tracked local environmental filters, with only a small or zero pure spatial fractions. Conversely, bacterial generalists in rock pools were controlled solely by environmental conditions (Székely & Langenheder, 2013). We obtained almost identical results for both habitat specialists and generalists. Both groups showed a consistently leading role for environmental processes in assemblage structuring in spring fens. However, clearly different results were obtained when analyses were run separately for specialists and generalists split into passive and active dispersers. Identical results were observed for active and passive generalists, but specialists showed a contrasting pattern. Active specialists (overall and within taxonomic groups) were controlled solely by environmental sorting, whereas spatial processes prevailed in passive specialists. Moreover, their variation explained by a pure spatial fraction was the highest of all groups.

Acknowledgments

We are very grateful to two anonymous referees as their valuable comments greatly improved the quality of this paper. We also thank to Ondřej Hájek for the preparation of the map. This study was supported by the research project of the Czech Science Foundation (P505/11/0779) and specific research of the Masaryk University (MUNI/A/0788/2013).

References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of the study area, field sampling, measurements of environmental variables, and a list of identification literature.

Figure S1. Rank abundance plots for six datasets showing the dividing points between common and rare species.

Figure S2. Variance partitioning run separately for three insect taxa divided according to their commonness and specialisation.

Figure S3. Variance partitioning run for three rare species matrices of all, passively, and actively dispersing species adjusted to the same information values as for the common species.

(Manuscript accepted 18 July 2014)