



# The importance of species replacement and richness differences in small-scale diversity patterns of aquatic macroinvertebrates in spring fens



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## ABSTRACT

This study provides new information on beta diversity (variation in species composition across space) of three invertebrate groups (Clitellata, Plecoptera, and Chironomidae) on a small, within-site spatial scale. It was conducted at small-sized spring fens where two contrasting mesohabitats, a flowing-water and a standing-water, can be clearly distinguished. Besides flow conditions, these habitats differed in the amounts of inorganic substratum and dissolved oxygen.

Factors related to flow conditions (dissolved oxygen and water temperature) influenced the composition of the studied assemblages at both mesohabitats, while substratum features were important at the standing-water habitat. The water chemistry was important for Clitellata at both mesohabitats and for Chironomidae at the flowing-water.

Using a new approach of disentangling beta diversity into two components (species replacement and species richness differences), clear difference in beta diversity patterns among the three assemblages were found, despite their roughly equal total beta diversities. Variation in species composition of those assemblages strongly limited by flow conditions (Plecoptera and partly Clitellata) was induced by differences in species richness, while replacement governed the variation in species rich assemblages that were able to utilise a wide range of conditions (Chironomidae and partly Clitellata). These results indicate that the size of species pool and the level of environmental filtering play an important role in forming beta diversity patterns, and caution that the same amount of beta diversity can be promoted by essentially different mechanisms, even at a very fine spatial scale with no involvement of dispersal limitations.

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## Introduction

Beta diversity, which is a variation in species composition across space, is one of the central concepts in community ecology and biogeography. Beta diversity represents a link between local (alpha) and regional (gamma) diversity and, in its simplest and most frequently used form it refers to a percentage of compositional dissimilarity (distance) of two communities (Veech et al., 2002; Anderson et al., 2011; Villéger et al., 2013). Recently, several reports have shown that distance-based beta diversity may be partitioned into two components: species replacement (turnover) and species

richness difference (Podani and Schmera, 2011; Carvalho et al., 2012, 2013). Partitioning beta diversity into the two components can provide a powerful tool for the analysis of the mechanisms that control species composition of taxonomical communities (Baselga, 2010, 2012; Carvalho et al., 2012; Tonial et al., 2012). As beta diversity partitioning appeared only recently, very little is known about the relative importance of the components for different taxonomic groups and different spatial scales. For example, at a large scale, the spatial pattern of deglaciation and postglacial colonisation from refugia caused a nested distribution of European land snails (Hausdorf and Hennig, 2003) and North American vertebrate assemblages (Dobrovolski et al., 2012). On the other hand, species replacement is expected to dominate on fine spatial scales (Hylland et al., 2005; Horsák and Cernohorsky, 2008; Carvalho et al., 2012; Tonial et al., 2012).

The relative importance of richness differences and species replacement is not random, but it rather relates to various species

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traits (e.g. dispersal ability or the ability to regulate body temperature; Baselga, 2010). Good dispersers, both active and passive (e.g. some microorganisms or birds), can effectively track all suitable habitats. Their beta diversity may then be generated by both richness differences and species replacement. In contrast, colonisation limitations of poor dispersers, such as amphibians, often lead to nested patterns due to species loss as one species moves away from refugia (Dobrovolski et al., 2012).

To date, most studies have focused on diversity patterns of vertebrates at large spatial scales (Baselga, 2010; Carvalho et al., 2012; Dobrovolski et al., 2012; Tonial et al., 2012), while invertebrates have been studied very poorly. Similarly, small-scale patterns are often neglected, even though small-scale variation can be driven by both niche-based and neutral-based processes (Anderson et al., 2011; Carvalho et al., 2012). In this study, our goal was to fill this gap and focus on the variation in species composition (beta diversity) of the assemblages of three ecologically distinct invertebrate groups (Clitellata, Plecoptera, and Chironomidae) on a small (within-site) spatial scale in spring fens.

Springs, while mostly small in size, represent a highly heterogeneous environment formed by an assortment of various aquatic and semi-aquatic habitats (see Glazier, 1991; Gathmann et al., 2008; Křoupalová et al., 2011; Cantonati et al., 2012). The variability in species composition of macroinvertebrate assemblages of springs has already been described, but mostly within a single large spring or spring system (Minshall, 1967; Wilhm, 1970; Ferrington et al., 1995; Křoupalová et al., 2011), while the heterogeneity of small springs remains virtually unknown.

We believe that understanding an ecological pattern within a variety of (ecologically different) taxonomic groups of organisms may enable to formulate general statements about the pattern in focus. Within this study, we analysed beta diversity patterns in three macroinvertebrate taxonomic groups that differ considerably in both their ecological demands and species pool sizes: Clitellata, Plecoptera, and Chironomidae (Diptera).

Clitellata, as the only of the three taxonomic groups, belongs to the permanent fauna and disperses passively. They are poorly documented at spring fens, but according to Bojková et al. (2011) they seem to be species-rich, comprising both aquatic and semiaquatic and soil species. Plecoptera, on the other hand, are strictly aquatic and prefer well-oxygenated cold running waters (Graf et al., 2009). They are usually scarce in spring fens and reach low species richness because of the absence of fast-flowing water and due to water level and temperature fluctuations (Langheinrich et al., 2004; Bojková and Helešic, 2009; Graf et al., 2009). Finally, Chironomidae have a terrestrial stage in common with Plecoptera but, in contrast, they are highly diverse, which gives them the ability to colonise most types of spring habitats and to dominate in many springs both in abundance and species richness (Lindegaard, 1995; Gerecke et al., 1998; Lencioni et al., 2011).

Specifically, we investigated among- and within-site variation in environmental factors and abundance and taxa richness of the three studied spring fen assemblages, i.e. Clitellata, Plecoptera, and Chironomidae. Subsequently, we focused on beta diversity at the flowing- and standing-water mesohabitats. Our main aims were (i) to draw an among-site comparison of studied mesohabitats and identify ecological gradients affecting the structure of the assemblages at the flowing- and standing-water; and (ii) to assess the contribution of species replacement and richness differences to the within site variation in the three assemblages (i.e. to the paired dissimilarities in the assemblage composition between the two mesohabitats). Two extreme patterns may be observed with any transition between them: (i) one mesohabitat that is the most suitable and harbours the majority of the species, leading to a nested pattern, or (ii) environmentally different mesohabitats are inhabited by different species, leading to a high contribution of

species replacement (Podani and Schmera, 2011; Carvalho et al., 2012).

## Materials and methods

### Study area and sites

The study area is situated in the Western Carpathians (Fig. 1) and includes two major parts: the Outer West Carpathians (the Czech Republic-Slovakia borderland and the Orava region in the north-western Slovakia in this study), which have flysch bedrock, and the northwestern part of the Inner Western Carpathians, which have a complicated geological structure. The flysch bedrock is made up of a rhythmic alternation of geological beds formed by sandstone and claystone layers. The beds differ in the proportional representation of sandstone and claystone and also in chemistry, which affects the water chemistry of the upwelling groundwater (Poprawa and Nemčok, 1988). The geological structure of the Inner Western Carpathians primarily includes cores of Paleozoic and crystalline schists overlaid by Mesozoic shale-sandstone and carbonate lithofacies. The water chemistry of the limestone areas is very similar to that of the Czech Republic-Slovakia borderland (Hájek and Hekera, 2005).

Spring fens of the Western Carpathians are usually small, treeless, and relatively distant from each other. The main ecological gradient in spring fens is that of mineral richness (i.e. changes in water chemistry that is dependent on the geological chemistry), which affects many taxonomic groups of organisms, such as vascular plants and mosses, Testacea, Mollusca, Clitellata, and Diptera (Hájek et al., 2002; Horsák and Hájek, 2003; Opravilová and Hájek, 2006; Bojková et al., 2011; Omelková et al., 2013). For this study, we selected 34 spring fens encompassing the entire range of the gradient of mineral richness. These sites can be classified into four ecological types according to typology based on vegetation (Hájek et al., 2006): (i) calcareous (tufa-forming) fens (thirteen sites), (ii) extremely mineral-rich fens without tufa precipitation (eight sites), (iii) moderately mineral-rich (*Sphagnum*-) fens (seven sites), and (iv) mineral-poor (*Sphagnum*-) fens (six sites).

### Field sampling and environmental variables

The studied spring fens were rather small in size (0.1–1 ha), but two considerably contrasting aquatic mesohabitats were easily distinguished at most sites. These mesohabitats differed mainly in flow conditions. The flowing water mesohabitat (mesohabitat A, the flowing-water) was formed by the uppermost part of a spring brook flowing from the spring source and represented the most stable part of a spring fen. The standing water mesohabitat (mesohabitat B, the standing-water) was a location with a waterlogged substratum and standing water, where the water level and temperature may fluctuate during season.

Samples were collected in spring (April–May) in 2006–2011. Each sample consisted of the upper layer of substratum and vegetation (approx. 5 cm thick) taken from a plot of 25 cm × 25 cm defined by a metal frame. At each spring fen, two samples were taken, one from each mesohabitat, giving a total of 68 samples. We believe that the selected sample size provided a reasonable estimate of the assemblages' taxonomic structure without causing any damage to the studied spring fens, which belong to the most endangered habitats throughout the whole Europe; mainly due to a rapid degradation and loss of fen habitats (Stanová, 2000; Horsák and Cernohorsky, 2008). Samples were elutriated through a net with a mesh size of 500 μm and fixed with 4% formaldehyde. The larvae of aquatic macroinvertebrates were hand-sorted and identified in the

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