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A naturally heterogeneous landscape can effectively slow down the dispersal of aquatic microcrustaceans

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Abstract:	<p>Several studies have suggested that aquatic microcrustaceans are relatively efficient dispersers in a variety of landscapes, whereas others have indicated dispersal limitation at large spatial scales or under specific circumstances. Based on a survey of a set of recently created ponds in an area of approximately 18×25 km, we found multiple indications of dispersal limitation affecting the community assembly of microcrustacean communities. Spatial patterns in the community composition were better explained by the geomorphological structure of the landscape than by mere geographic distances. This suggests that ridges separating the network of valleys act as dispersal barriers, and as such may channel the dispersal routes of the studied taxa and, likely, of their animal vectors as well. Dispersal limitation was further supported by a strong positive relationship between species richness and the abundance of neighbouring water bodies, suggesting that isolation affects colonization rates. Finally, the apparent dispersal limitation of microcrustaceans is further corroborated by the observation of low colonization rates in newly dug experimental ponds in the study area.</p>	

A naturally heterogeneous landscape can effectively slow down the dispersal of aquatic microcrustaceans

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PJJ, SAJD and AP proceeded the statistical analyses. PJJ, AP and SAJD wrote the
manuscript.

ABSTRACT:

Several studies have suggested that aquatic microcrustaceans are relatively efficient dispersers in a variety of landscapes, whereas others have indicated dispersal limitation at large spatial scales or under specific circumstances. Based on a survey of a set of recently created ponds in an area of approximately 18×25 km, we found multiple indications of dispersal limitation affecting the community assembly of microcrustacean communities. Spatial patterns in the community composition were better explained by the geomorphological structure of the landscape than by mere geographic distances. This suggests that ridges separating the network of valleys act as dispersal barriers, and as such may channel the dispersal routes of the studied taxa and, likely, of their animal vectors as well. Dispersal limitation was further supported by a strong positive relationship between species richness and the abundance of neighbouring water bodies, suggesting that isolation affects colonization rates. Finally, the apparent dispersal limitation of microcrustaceans is further corroborated by the observation of low colonization rates in newly dug experimental ponds in the study area.

INTRODUCTION:

Dispersal limitation and its impact on the community assemblage of isolated natural communities remains an intensively studied topic since the original formulation of the Island Biogeography Theory (MacArthur and Wilson 1967). Organisms with limited dispersal capabilities in particular should be studied in a regional rather than local context (see Hanski 1998, Leibold and Norberg 2004). Inhabitants of inland aquatic habitats, which are assumed to be physically more separated than terrestrial environments, have been reported to have larger dispersal capacities than terrestrial taxa of the same taxonomic groups (Kappes et al. 2014). Within the terrestrial realm, spatial structuring at very local scales is particularly obvious for soil organisms (e.g., Jiménez et al 2014), which are usually more dispersal limited

than their above-ground relatives (Lindo and Winchester 2009). However, the majority of terrestrial passive dispersers, including plants (e.g., Auffret and Plue 2014, Soons and Ozinga 2005, Nathan and Muller-Landau 2000) and various invertebrates (see review Bell et al. 2005), can be quite effectively transported by wind or animal vectors. Such taxa tend to be more dispersal limited when they are habitat specialists (e.g., Ellis 2012, Löbel et al. 2006, Brunet et al. 2011) or at biogeographic rather than regional scales (e.g., Gonçalves-Souza et al. 2014).

Passive dispersal is one of the key adaptations of life in isolated freshwater habitats (see Maguire 1963), and has been studied in a considerable number of aquatic invertebrates (see Beisner et al. 2006, Bohonak and Jenkins 2003) and plants (e.g., Alahuhta et al. 2014, Viana et al. 2014). Microcrustaceans, especially cladocerans and copepods, are frequently studied model groups both in the field and in outdoor mesocosm experiments. Most studies on microcrustaceans have focused on relatively small spatial extents (at the scale of kilometres or less), and have found microcrustaceans to be efficient dispersers (e.g., Cohen and Shurin 2003; Michels et al. 2001). On the contrary, at very broad spatial scales (hundreds to thousands of kilometres) a limited number of studies have suggested some level of dispersal limitation (e.g., De Bie et al. 2012; Zhai et al. 2015). Under some specific circumstances, evidence of dispersal limitation at smaller spatial scales has also been reported from both experiments (Jenkins 1995) and field-based observational studies (Soininen et al. 2007). At intermediate scales (tens of kilometres), Declerck et al. (2011b) found growing spatial structuring with increasing spatial scale. However, field studies assessing potential dispersal limitation among microcrustacean communities at such intermediary scales are rare.

In our study, therefore, we evaluated to what extent dispersal of microcrustaceans to newly created aquatic habitats can be affected by landscape structures that may act as potential barriers for passive dispersal. Over an area of ca 18×25 km, we studied 42 newly

created fishless and spatially clustered pools (Fig. 1) in a landscape with four important characteristics: 1) a lack of large water bodies, 2) low connectivity among aquatic habitats; 3) a relatively low density of waterfowl (Šťastný et al. 2006), known to be one of the most important vectors of microcrustacean dispersal (Figuerola and Green 2002); and 4) the presence of steep canyons that can restrict the movement of dispersal vectors, including both waterfowl and terrestrial mammals. We focused on the species richness and composition of three major taxonomic groups of microcrustaceans (cladocerans, copepods, and ostracods).

In this naturally fragmented landscape, we hypothesized that the local species richness and composition of microcrustaceans should be structured more by the landscape structure (i.e., by natural spatial clustering and connectivity of the pools determined by the topography) than by pure geographical distance. Alternatively, if dispersal was unlimited we expected to observe only weak spatial patterns (if any), which could not be explained by the environment. Consequently, we also analyzed multiple statistical models that took into account the effects of potentially confounding environmental variables (which may be also spatially structured) and the species composition of invertebrate predators in the studied pools. Under the assumption of dispersal limitation, we also expected microcrustacean species richness in young pools to be related to the number of other aquatic habitats in the neighbourhood of the studied localities, which likely serve as the source of immigrant species (Louette and De Meester 2005). To evaluate this migration we also performed a field experiment with new pools dug directly in the study area. Three independent aspects make this study unique in the context of other spatially-oriented analyses of microcrustacean metacommunities: 1) the intermediate spatial scale, which is underrepresented in other studies; 2) the taxonomic coverage; and 3) the heterogeneous landscape structure.

METHODS:

Study site and localities

The 42 studied pools, selected according to their position, size and age, are located within the Kokořínsko Protected Landscape Area (ca 18×25 km, N 50° 23'-50° 38' , E 14° 24'-14° 42'), Czech Republic (Fig. 1). The local landscape is mostly forested and consists mainly of deep and narrow rocky valleys (with depths often reaching about 100 m), the alluvial plains of two larger streams, as well as open meadows and fields located at higher elevations. Moreover, this area is characterized by a sparse stream network (due to the sandstone subsoil; see inset in Fig. 1) and scarcity of large aquatic habitats. Subsequently, there is also a relatively low abundance of waterfowl (Šťastný et al. 2006), key long-distance vectors of aquatic invertebrates and plants (Figuerola and Green 2002). The pools were created between 1997 and 2004 for conservation purposes, to provide suitable habitats for vulnerable amphibian, invertebrate and macrophyte taxa. Most of them (34 pools, i.e., 81%) were new, the remaining ones (8 pools, 19%) were renewed at places where a pool or a wetland had been located in recent decades but more recently had no open-water habitat remaining.

The pool surface areas spanned several orders of magnitudes (see Supplementary Table S1), with maximum values per pool in the studied years (2005 & 2006) varying from 0.5 to 2400 m² (median 150 m²). Maximum pool depths varied from 0.2 to 2 m (median 0.85 m). Seven pools are connected to very small streamlets, while the remainder are not connected to any running water, even during occasional spring floods. Two of the pools occasionally dry out if the groundwater level is too low in summer; all of them freeze over in winter. All pools were intentionally kept fishless for the whole study period to promote the diversity of other animal and plant taxa. All also contained at least some macrophyte stands or littoral vegetation. More details on the basic environmental parameters of each pool are given in Supplementary Table S1.

Field sampling and sample processing

The pools were sampled in two consecutive years (2005-2006), three times per year: in spring (late April to early May), summer (July) and autumn (October to early November). Two pools were completely dry in summer 2006, and three samples were accidentally lost during the fieldwork; we thus processed altogether 252 samples. We used plankton nets with mesh sizes of 40 to 200 μm to collect samples of microcrustaceans (cladocerans, copepods, and ostracods). The 200 μm throwing net was used to collect samples from open water; a pole-attached 100 μm net was swept through the littoral vegetation (the finer mesh size ensuring that even the smallest chydorid cladocerans living in the vegetation were collected). These samples were preserved in 90% ethanol. Furthermore, we collected a formalin-preserved sample at every site (primarily for an independent analysis of rotifer species composition but also to validate the presence/absence of crustacean species). When the macrophyte cover of the pond area exceeded 25% but open water was also present, both 100 μm and 200 μm net samples were taken and inspected separately; results were then pooled for the respective pond during the data analyses. The plankton nets were carefully washed between sampling of different pools.

During each sampling, we measured water temperature, dissolved oxygen concentration, conductivity and pH with a multiparameter water quality probe (YSI 556 MPS, YSI Inc., *Yellow Springs*, USA) in the middle of the water column. However, only conductivity was used in further statistical analyses, as the other parameters substantially vary on a diurnal basis. Coverage of macrophytes was rated categorically, as low (up to 25% of the pool bottom), medium (25%–75%) and high (over 75%). Pool depth and approximate surface area were also noted on each sampling date.

Chlorophyll a, nitrogen and phosphorus levels were not measured in 2005 and 2006, but we had the opportunity to measure these variables during a later sampling campaign in

spring 2008, when all other measured characteristics and the overall appearance of the pools were very similar to preceding years. In these samples, total nitrogen and total phosphorus were analysed from water filtered through plankton net of 40 µm mesh size to remove large seston. Nitrogen was then analysed by high temperature combustion using a Formac Total Organic Carbon/Total Nitrogen analyzer (Skalar Analytical B.V., Breda, Netherlands). Total phosphorus was measured colorimetrically after perchloric acid digestion according to Kopáček and Hejzlar (1993). Chlorophyll a level was estimated in vivo with an AquaFluor Fluorometer (Turner Designs, Sunnyvale, USA) and regarded as an indicator of the overall trophic state and food availability for herbivorous microcrustaceans.

Microcrustacean species were identified under a light microscope and stereomicroscope; copepods and ostracods were first treated with lactic acid to improve the observation of detailed morphological traits. Whenever possible, animals were identified to the species level using Amoros (1984), Flößner (2000), Šrámek-Hušek (1953), Meisch (2000), Einsle (1996) and several unpublished keys on local fauna. In a few samples, too small and therefore undeterminable copepod larvae were observed; these were not included in further analyses. Whenever possible, at least 300 individuals from sub-samples of known volume were identified from each sample, otherwise all specimens were identified and counted. In open water samples, *Chaoborus* larvae were frequently found together with microcrustaceans. As these predators are known to influence their communities substantially (e.g., Jäger et al. 2011; Luecke and Litt 1987; Yan et al. 1991), the relative abundance of *Chaoborus* within the sample was used in the analyses as a semi-quantitative variable (modified from Braun-Blanquet scale (Braun-Blanquet et al. 1932) and consisting of seven categories: <1%, 1–5, 5–10, 10–20, 20–40, 40–80, ≥80%).

To evaluate potential predation pressure on microcrustacean communities, we simultaneously took samples of other macroinvertebrates living in the pools using a sweep

net. These were always collected by the same person, applying a standardized sampling effort (15 minutes sampling time per site). According to the local conservation policy, the sampling of invertebrates had to be performed in order to maximize species richness but not to collect macroinvertebrates quantitatively; thus neither the abundance nor biomass of individual species could be quantified. Therefore, data on potential predatory taxa present in the sampled pools, i.e., true bugs, dragonfly larvae, and aquatic beetles, were available as presence/absence data only (Supplementary Table S2). All these taxa were identified by experts on the respective groups (see Acknowledgements).

Data analysis

The main aim of our analyses was to evaluate the extent to which colonization of newly constructed ponds by microcrustacean zooplankton may be constrained by dispersal limitation. This was achieved through multiple analyses of microcrustacean community composition data, as well as through the analysis of species richness patterns.

We created three sets of a priori spatial predictors based on pool locations and topography to evaluate potential dispersal limitation. Categorical dummy variables identified clusters of pools (Fig. 1), within which we hypothesized among-pond dispersal is more frequent than among different clusters. In addition, for all pairs of the pools we computed two geographic distance matrices: a Euclidean distance matrix from geographical coordinates, and a distance matrix that will further be referred to as the "valley distance" matrix. The latter matrix comprised the shortest distances measured between each pair of pools following the course of the main canyons and valleys. We hypothesized that this "valley distance" would reflect connectivity among the localities by animal vectors (particularly terrestrial ones, which we assumed play a major role in the area). These expectations were made a priori, without any information on existing patterns of community differentiation. From both distance

matrices, we calculated principal coordinates (PCoA) and used the most important orthogonal axes (vectors) with positive eigenvalues according to Borcard et al. (2011). Given that the probability for a pond to be reached by species may also depend on the availability of source populations in the neighbourhood, we also quantified the number of all lentic aquatic habitats present in a radius of 3 km around each pool (according to Louette et al. 2008). We applied partial redundancy analysis (RDA) and the variation partitioning procedure of Peres-Neto et al. (2006) to assess the unique explanatory power of each type of spatial predictor variable groups and the strength of their collinearities. Finally, we created a spatial RDA model composed of the variables with significant contributions.

To assess how much the community structure reflects the spatial structure and how much is confounded by variables related to other important ecological processes, we performed a second variation partitioning to challenge the spatial model with two categories of other explanatory variables: (1) a set of environmental variables (the ‘environmental’ matrix) and (2) variables representing features of the invertebrate predator communities (the ‘predator’ matrix).

The environmental matrix included key characteristics of the aquatic environment potentially affecting zooplankton communities, i.e. phytoplankton chlorophyll a concentration, concentration of total nitrogen and phosphorus, conductivity, a binary variable representing the historical presence/absence of a water body at the site, the age of the pool, macrophyte cover, surface area, and maximum depth. This matrix also included information on the characteristics of the immediate neighbourhood, i.e., the presence or absence of a connection to a stream, position of the pool at the bottom of a canyon or permanently shadowed area. The predator matrix contained variables reflecting various aspects of invertebrate predation pressure and consisted of predator species richness, semi-quantitative density of *Chaoborus* larvae in open water samples, and five variables representing the major

axes of variation in the species composition of invertebrate predators (i.e. the five most important PCoA axes built from a Sørensen dissimilarity matrix that was calculated from predator presence-absence data).

Presence-absence data indicate the spatial distribution patterns of species. When based on abundance data, the interpretation of patterns of community differentiation may be confounded by the relative ecological success of species at sites, as well as possible sampling bias when using different mesh sizes. For this reason, we expected presence-absence data to be more straightforward for the interpretation of metacommunity patterns that had been caused by dispersal limitation (Declerck et al. 2011b). All RDA and variation partitioning analyses in this study were therefore based on microcrustacean presence-absence data. To avoid the problem of too many zeros in the presence-absence data (the so-called double-zero problem), we applied the procedure of distance-based redundancy analysis (Borcard et al. 2011; Legendre and Anderson 1999). We first compiled species lists for each site based on all observations of our two-year study period. We then used this presence-absence matrix to calculate a Jaccard distance matrix, and subsequently extracted principal coordinates which were then used as species variables in the redundancy and variation partitioning analyses. To prevent negative eigenvalues, we applied a Lingoez correction in these principal coordinate analyses. All continuous environmental explanatory variables were log-transformed prior to analyses. Prior to variation partitioning, we applied the AIC stepwise forward selection procedure according to Crawley (2007) on the environmental and predator variables, using the R function "step". Variation partitioning was computed using the functions "vegdist" and "varpart" of the R library vegan (Oksanen et al. 2011). Principal coordinate analysis was done using the function "pcoa" of the package ape (Paradis et al. 2004).

To identify and evaluate the most important variables affecting crustacean species richness, we constructed a regression tree relating local species richness with the entire set of

explanatory and spatial variables. Regression trees are appropriate for exploring complex data including multiple and unknown interactions (e.g., Allen and Dodson 2011; Davidson et al. 2012). To construct the tree, we applied binary recursive partitioning using the R library tree (Ripley 2011); afterwards we reduced the model complexity by using the function “prune.tree” based on a cost-complexity measure according to Crawley (2007).

Colonization experiment

We complemented our survey with a colonisation experiment based on the expectation that colonization of newly created habitats represents a lower boundary of dispersal rates. We built a set of 20 experimental pools in an area of 120 x 160 m in a meadow within the study area (Fig. 1). The pools had a circular shape of 5 m in diameter, with an average depth of ca 0.5 m and a surface area of approximately 10 m². The bottom of the pools was covered by plastic foil to reduce variations in water level fluctuation among pools. Pools were filled with water from a nearby brook that had been double filtered through a plankton net (40 µm mesh). For the sake of other research objectives, half of the experimental pools were inoculated with 500 adult females of *Daphnia curvirostris* per pool (manuscript in preparation); these units were not taken into account for the present study. We were able to collect data from only 8 of the remaining pools because two dried out soon after the start of the experiment due to damage to the foil.

Sampling of the pools started four weeks after pool construction (July 2007). A 6 l water sample from the whole water column was collected at multiple places in each pool using a tube sampler, and filtered through a plankton net with 40 µm mesh size. Samples were then preserved with formalin. To avoid contamination, the equipment was carefully washed between sampling of different pools. For each pool, crustacean species composition (presence/absence) was analysed from six samples collected in the first year of the existence

of the pool (collected in three-week intervals between August and December 2007), and five samples from the second year (collected in ca two-month intervals between March and December 2008).

In addition, we sampled all water bodies within a radius of 3 km of the colonisation experiment, assuming that these water bodies were the most likely candidate sources of microcrustaceans colonizing the experimental pools (except for *D. curvirostris*, which could colonize from adjacent inoculated pools). These water bodies consisted of five pools from cluster F (Fig. 1, no. 37-41; distance: 0.5-2 km), one small pond in a castle park (P1; distance: ca 3 km) and a set of 5 interconnected shallow fishponds (P2; 0.2-2 ha; distance: 2-3 km). We are not aware of any other relevant freshwater habitats located closer than 6.2 km to the experimental area. We assessed the local species pool from these water bodies by sampling them once during the spring and once during the summer during the experiment, except for pools 37-41 that were regularly sampled in the framework of the survey described above.

RESULTS:

Microcrustaceans found in the pools

We identified 54 microcrustacean taxa (Supplementary Table S3): 30 species of cladocerans, 15 cyclopoids, 1 calanoid, and 8 ostracods. The most common species were the cyclopoids *Eucyclops* gr. *serrulatus* (40 pools) and *Megacyclops viridis* (26 pools), the cladocerans *Chydorus sphaericus* (40 pools) and *Simocephalus vetulus* (30 pools), and the ostracods *Cypridopsis vidua* (30 pools) and *Notodromas monacha* (28 pools). One of the cladocerans found during this study, *Daphnia hrbaceki*, was recently described as a new species (Juračka et al. 2010), and the most common cyclopoid, *E. gr. serrulatus*, was shown to actually be a diverse species complex (Hamrová et al. 2012).

The average number of species per sample reached 4.4, whereas the maximum species count in a single sample was 13. However, the cumulative species richness per pool over the whole study period ranged from 7 to 21 species (mean 11.7; see Supplementary Table S1). Pools created up to 2 years before the onset of the study (n=17) already hosted relatively rich microcrustacean communities (7-19 spp., median 12), and the species richness of this category of young pools was not significantly lower or higher than that of older pools (n=25, 8-21 spp., median 11).

Variation partitioning of community composition

Valley distances were superior to Euclidean distances in explaining variation in the microcrustacean community composition (adj. R^2 of conditional effect: 7%, $p < 0.005$ for the former vs. 0.7%, $p = 0.24$ for the latter; results not shown). Valley distances (Fig. 2A; adj. R^2 of the conditional effect: 6.7%; $p < 0.005$), and *a priori* defined spatial clusters (Fig. 2A; adj. R^2 of the conditional effect: 4.0%; $p = 0.035$) each explained a significant portion of the compositional variation independently. The conditional effect of neighbouring source habitats was lower and insignificant (Fig. 2A; adj. R^2 of the conditional effect: 1.0%; $p = 0.095$). However, the number of neighbouring habitats was significantly collinear with both previously mentioned spatial matrices (Fig. 2A; adj. R^2 of the marginal effect: 2.6%; $p < 0.005$). Subsequently, we merged all three predictor variable categories into one matrix (further referred to as the 'spatial context') and partitioned the crustacean community variation among this matrix and the most parsimonious predictor matrices for pool environment (consisting of the variables pool surface area and hydrological history) and invertebrate predator communities (i.e., number of predator taxa). Each of the three matrices (spatial, environmental, predator) explained the crustacean species composition significantly when tested on their own (marginal effects: $p \leq 0.005$; Fig. 2B). Spatial context explained a

total of 11.7% ($p < 0.005$) of the community variation, of which 6.7% ($p < 0.005$) was unique and of which 5% was collinear with the other predictor variables. Environmental variables explained a total of 7.4% ($p < 0.005$) of the community variation, of which 2.2% ($p < 0.05$) was collinear. Predator species richness explained 6.7% ($p < 0.005$) of the microcrustacean species composition, but all of this variability was found to be collinear with the spatial and environmental variables. Indeed, a strong positive association was found between pool surface area and predator species richness (Fig. 3). The whole model explained 16% of the microcrustacean community variation and was highly significant ($p < 0.005$).

Species richness

The best regression tree (Fig. 4) explained 64% of the variation in local species richness. The strongest predictor of this tree, explaining 36% of species richness variation, was the number of lentic aquatic habitats within a 3 km-radius around the target pools. The 20 pools surrounded by less than 8 potential source habitats hosted significantly fewer microcrustacean species than the remaining 22 pools (median values of 10 and 13.5 species, respectively). The latter group was further split into a group of 10 smaller, relatively species-poor pools (surface area: $< 200 \text{ m}^2$; median of species richness: 12 species), and 12 larger pools with higher species richness (median: 14 species). Macrophyte cover was identified as the most important variable affecting the species richness in pools with low numbers of nearby source habitats. Pools with a macrophyte cover lower than 25% of the pool surface area had lower species richness (median: 9 species) than pools with a higher macrophyte cover (median: 11 species). Pool surface area, the number of nearby source habitats, and macrophyte cover all showed positive associations with species richness (see Fig. 4).

Colonization experiment

During the two surveyed seasons, the ensemble of experimental pools was colonized by a total of six microcrustacean taxa (Supplementary Table S4), two found very early after the start of the experiment and four additional ones in the course of the second year (Fig. 5). The number of taxa observed at any point in time was usually very low (Fig. 5). *D. curvirostris*, which most probably originated from the nearby inoculated pools, was found in four pools already during the first sampling, then colonizing one more pool one month later, and an additional one in the second year. Other early colonizers were the cladoceran *Bosmina longirostris* (found in two pools on the first sampling date) and juvenile copepods (in four pools; these, however, could not be identified to the species level). Copepod adults, identified as *Mesocyclops leuckartii* and *Eucyclops* gr. *serrulatus*, were found in the second year of the study (each in two pools). Additional taxa observed during the second year included one cladoceran (*Scapholeberis mucronata*, in two pools), and an ostracod (*Notodromas monacha*, eventually found in seven pools). All these species were also found in pools of the field survey (Supplementary Table S4).

DISCUSSION:

In a landscape characterised by scarce freshwater habitats located within valleys demarcated by steep slopes, we aimed to evaluate the extent to which the colonisation process of microcrustacean communities in newly created pools may be hampered by dispersal limitation. Three independent lines of evidence indeed suggest some level of dispersal limitation: (1) A priori defined clusters of the pools, based on their location in canyons or deep valleys, significantly predicted microcrustacean species composition. Also, valley distances explained community composition substantially better than Euclidean distances between pools. (2) Pools with more aquatic habitats in their vicinity contained more species than more isolated ones, suggesting that microcrustacean communities in the pools are

substantially influenced by dispersal from nearby sources. (3) In an outdoor colonization experiment, only a very limited subset of the local microcrustacean species pool (6 out of 31 spp.) was able to successfully colonize newly created ponds within a time span of 1.5 years.

The degree to which a metacommunity of organisms is affected by dispersal limitation depends on the age of the habitat, distances between habitat patches, and the presence and spatial configuration of dispersal barriers, in addition to other important factors such as overall landscape connectivity and the dispersal capabilities of the organisms under consideration (Leibold et al. 2004). Our study is unique in that it addresses spatial community patterns of relatively young microcrustacean communities at an intermediate geographic scale (tens of kilometres). In contrast, most studies on young communities have so far been largely experimental, based on the monitoring of community trajectories in mesocosms or newly dug ponds within short time frames and at very local scales (e.g., Cohen and Shurin 2003; Jenkins 1995). Survey-based studies of cladoceran metacommunities at larger scales have mainly been limited to an analysis of the spatial structure of older, established metacommunities (e.g., Declerck et al. 2011b; Viana et al. 2014). Although experimental studies have often documented the rapid colonization of newly created pond habitats at least by a regionally occurring subset of crustacean zooplankton species (e.g., Cohen and Shurin 2003; Louette et al. 2008; but see Jenkins and Buikema 1998), several survey-based studies have also revealed indications of some degree of dispersal limitation in naturally occurring established zooplankton metacommunities. For example, in studies of habitats spatially arranged in a hierarchic manner, Ng et al. (2009) and Declerck et al. (2011b) reported an increased signature of dispersal limitation with increasing spatial extent. Our study therefore fills a gap by studying the signatures of dispersal limitation in recent pond habitats at larger than local spatial scales.

Studies comparing spatial patterns among organism groups have indicated weaker spatial patterning in zooplankton taxa when compared to larger-bodied passively dispersing organism groups such as macroinvertebrates and fish, but stronger patterning than in microorganisms (Beisner et al. 2006; De Bie et al. 2012; Shurin et al. 2009). For recently established pond habitats, our results suggest that the zooplankton assembly can be substantially affected by dispersal limitation, to such an extent that the signature of this dispersal limitation is still noticeable several years after pond creation. It should be noted, however, that our study may only be representative for pools and ponds in landscapes that are characterized by a low abundance of freshwater habitats and the presence of important dispersal barriers. Furthermore, at longer time scales, the impact of dispersal limitation might be weaker, and community composition will likely better reflect environmental conditions (the so-called "quorum effect"; see Jenkins and Buikema 1998), possibly mediated by priority effects (Allen et al. 2011).

Abiotic vectors, such as wind, rain or water currents, have occasionally been shown to play a role in the overland dispersal of crustacean zooplankton organisms at small spatial scales (e.g., Cacères and Soluk 2002; Cohen and Shurin 2003; Sciullo and Kolasa 2012). Given the relatively large spatial scale of our study area and the low hydrological connectivity among pool habitats, animal vectors most likely played an important role in crustacean dispersal. The most important candidate vectors in the area are large mammals (e.g., Vanschoenwinkel et al. 2008b; Waterkeyn et al. 2010), and waterfowl (e.g., Figuerola and Green 2002); other animal groups reported to disperse freshwater crustaceans, such as amphibians (Vanschoenwinkel et al. 2008a) and large aquatic insects (Schlichting and Sides 1969; Van de Meutter et al. 2008), are probably less relevant. Large mammals, particularly roe deer and wild boar, are locally abundant (Beran et al. 1999), and their footprints were often observed at the edge of studied pools during the sampling. Despite relatively low

waterfowl densities in the region when compared to the rest of the Czech Republic, we also frequently observed mallard ducks (*Anas platyrhynchos*) at the studied localities, known to disperse dormant stages of aquatic invertebrates (Green et al. 2002; Proctor 1964) and even living ostracods (Green et al. 2013). Thus, waterfowl may contribute to pool colonization, and the signs of dispersal limitation may rather represent the limited mobility of vectors among pools from different clusters than their overall scarcity.

The amount of community variation that was explained by local environmental variables was low. Such low explanatory power of environmental variables may occur when important latent environmental variation is missed by the survey, and when spatial processes influence the species composition more than species sorting (Padial et al. 2014). Furthermore, priority effects (Frisch and Green 2007) and habitat monopolization (De Meester et al. 2002; Louette et al. 2007) by first colonizers may also contribute to a poor match between environment and species composition (Jenkins and Buikema 1998; Schulz et al. 2012). Pool surface area and hydrological history of the habitat were the only abiotic environmental variables that we found to be significantly associated with microcrustacean community composition. The variation explained by these factors was, however, almost entirely collinear with the taxonomic richness of predatory invertebrates and spatial context (Figs 3 and 4). Indeed, ponds with a large surface area contain a more diverse invertebrate fauna than smaller ponds (Angeler and Alvarez-Cobelas 2005; Anusa et al. 2012; March and Bass 1995).

Splitting the explained variability of the species composition into spatial and environmental contexts via variation partitioning based on eigenvector-based spatial filters (including PCoA used by us) has been recently disputed, as this approach may lead to inaccurate estimations of explained variability when inappropriately used (e.g., Diniz-Filho et al. 2012, Gilbert and Bennett 2010, Smith and Lundholm 2010). After reviewing numerous variation partitioning studies, Soininen (2014) strongly suggested considering not only spatial

and environmental matrices, but also biotic interactions, which may mask a species sorting mechanism (i.e., the effect of the "environment fraction" on the species composition). In our study, we indeed analysed data on predator presence that may have influenced the observed communities substantially (e.g., Shurin 2001, Verreydt et al. 2012). Furthermore, our conclusions that microcrustacean dispersal is limited in the studied heterogeneous landscape are based not only on variation partitioning of the species composition, but also on the analysis of species richness.

During our entire study, we detected a total of 54 taxa for the whole region under consideration, which is in agreement with the only previous study on microcrustaceans in the area (Omesová 2005), which reported 24 cladocerans and 16 copepods from 30 comparable habitats. Regression tree analysis revealed that microcrustacean species richness in ponds was best related to the number of other aquatic habitats in the immediate surroundings. This pattern most likely reflects the decreasing likelihood of colonization of a pond with an increasing degree of isolation. The pool area was the second most important factor influencing microcrustacean species richness, with larger pools being more species-rich than smaller pools. Populations in larger pools are less prone to extinction than populations in smaller pools (Frisch et al. 2006) and have a higher probability of receiving dispersing propagules than small patches (e.g., MacArthur and Wilson 1967). Larger pools may also harbour higher microhabitat diversity and therefore provide higher niche diversity, allowing the coexistence of higher numbers of species (March and Bass 1995). The positive association between macrophyte cover and species richness indeed suggests an important influence of microhabitat diversity for crustacean diversity in these ponds (e.g., Cornell and Lawton 1992; Declerck et al. 2011a; Declerck et al. 2007; Shiel et al. 1998).

Despite the absence of active transport, documented colonization rates of microcrustaceans colonizing new habitats are usually relatively high, at least at small to

intermediate spatial scales (e.g., Frisch et al. 2012, Louette and De Meester 2005). Our study demonstrates that in sufficiently complex landscapes with a low density of and connectivity among waterbodies, microcrustacean communities may be substantially affected by dispersal limitation, at least in the early stages of their existence. The application of distance measures that take into account the landscape complexity, such as the "valley distance" used in our case, can help elucidate scale-dependent biodiversity patterns.

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CAPTIONS OF FIGURES AND SUPPLEMENTARY MATERIAL:

Fig. 1: Position of the studied localities (n=42) within the heterogeneous landscape, and their affiliation to spatial clusters (n=6) defined by pool geographical position in relation to deep canyons representing potential barriers for dispersal vectors, and by connectivity by streams. The small inset map shows the position of the studied area within the river network of the Czech Republic

Fig. 2: Venn diagram with variation partitioning results of microcrustacean species composition explained by: a) three spatial variable categories (i.e., affiliation of pools to a priori defined clusters, the number of other lentic habitat within a radius of 3 km, and principal coordinates of the ‘valley’ distance dissimilarity matrix); b) three variable categories representing spatial context, pool characteristics, and invertebrate predator richness. **: values significant at the 0.005 level; *: 0.05 level (tested with partial RDA at 200 permutations)

Fig. 3: Relationship between the invertebrate predator species richness and pool surface area

Fig. 4: a) Regression tree identifying the most important variables influencing the microcrustacean species richness within each of the studied pools. This tree explains 63.7% of the variation in species richness. Boxplots under each tree node compare species richness between groups of the pools defined by these nodes. b) Relationship between species richness and the most important variables selected in the regression tree

Fig. 5: Microcrustacean species richness in experimental pools (n=20) in a meadow within the study area, since their creation in August 2007 until December 2008. Whiskers above the

755 line showing species richness per pool indicate standard errors of the mean. The dashed line
756 represents the number of species actually observed in all experiment pools for the specific
757 month, while the grey line shows a cumulative curve of the same number

a)

b)

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