

# ECOGRAPHY

## Research article

### How pondscapes function: connectivity matters for biodiversity even across small spatial scales in aquatic metacommunities

Barbara Barta  <sup>1,2</sup>, Attila Szabó <sup>1,3</sup>, Beáta Szabó <sup>1</sup>, Robert Ptacnik <sup>4</sup>, Csaba F. Vad <sup>1,5,\*</sup> and Zsófia Horváth <sup>1,5,\*</sup>

<sup>1</sup>Institute of Aquatic Ecology, HUN-REN Centre for Ecological Research, Hungary

<sup>2</sup>Doctoral School of Biology, Institute of Biology, ELTE Eötvös Loránd University, Budapest, Hungary

<sup>3</sup>Swedish University of Agricultural Sciences, Uppsala, Sweden

<sup>4</sup>WasserCluster Lunz, Lunz am See, Austria

<sup>5</sup>Laboratory of Aquatic Ecology and Evolutionary Biology, KU Leuven, Leuven, Belgium

Correspondence: Barbara Barta ([barta.barbara@ecolres.hu](mailto:barta.barbara@ecolres.hu))

#### Ecography

2024: e06960

doi: [10.1111/ecog.06960](https://doi.org/10.1111/ecog.06960)

Subject Editor: Jason Pither

Editor-in-Chief: Miguel Araújo

Accepted 9 October 2023



Habitat loss and fragmentation are growing global threats to natural habitats and their networks, posing significant challenges to biodiversity conservation. Globally, ponds are sharply declining in number because their small size makes them highly vulnerable to land use changes. While it is generally agreed that connectivity in habitat networks is crucial for sustaining biodiversity, the effect of connectivity on biodiversity patterns over small-scaled habitat networks has so far received less attention given the general assumption that metacommunities lack spatial structuring on small scales. In this study, we tested whether this holds for multiple passively and actively dispersing organism groups in a well-delineated pond metacommunity of 54 bomb crater ponds situated within 1 km. We investigated the influence of space and environment on species richness and metacommunity structure in these ponds, which share similar age, size, and shape and are subject to strong environmental gradients, making it an ideal study system. We specifically examined the impact of network centrality on taxonomic richness and eigenvector-based spatial arrangement on metacommunity structure across different organism groups, including prokaryotes, microeukaryotes, zooplankton, macroinvertebrates, and amphibians. We found that while environmental filtering is the primary driver of community dynamics, there is also a significant spatial signal, particularly for passively dispersing groups, demonstrating the role of the central-peripheral connectivity gradient. These findings highlight the importance of studying and protecting ponds as parts of a network rather than focusing on individual ponds.

Keywords: centrality, dispersal, invertebrates, multi-group, spatial network, zooplankton



[www.ecography.org](http://www.ecography.org)

© 2023 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

\*Shared senior authorship.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

## Introduction

Connectivity in habitat networks is a major driver of local and regional biodiversity patterns via species dispersal (Taylor et al. 1999, Leibold et al. 2004, Fletcher et al. 2016). Among discrete habitat patches, such as ponds, connectivity is frequently approximated as a function of distance, where the highest levels of dispersal are assumed among neighbouring habitats (Calabrese and Fagan 2004). Across small spatial scales, i.e. up to a few hundred meters, dispersal levels are generally assumed to be high enough to efficiently counteract local extinction events, thereby contributing to efficient species sorting (Langenheder and Lindström 2019). Within a few meters, e.g. in rock pool metacommunities, occasional biotic homogenisation may occur via mass effects, resulting from extremely high dispersal rates (overspill; Vanschoenwinkel et al. 2007). The relevance of these processes, however, decays rapidly with increasing distance and most natural metacommunities are rather assembled along a gradient of intermediate to low dispersal, depending on the actual spatial scale, landscape connectance, and species traits (Leibold and Chase 2018). While there is a general agreement on the importance of sufficient connectivity in habitat networks for the sustenance of biodiversity, its above-mentioned scale and context dependence and their effect on biodiversity patterns remain lesser understood.

Pondscapes are regional networks of ponds clustered in a landscape (Biggs et al. 1994, Boothby 1997, Baguette et al. 2013). Since the introduction of the term, it has been frequently argued that ponds function as habitat networks, e.g. by serving as stepping stones for aquatic taxa (Pereira et al. 2011), and that their value for biodiversity lies in their numbers (Oertli et al. 2002, Martínez-Sanz et al. 2012). Pondscapes are shrinking worldwide, which increases the isolation between the remaining habitats (Thornhill et al. 2018). These changes are predicted to result in biodiversity loss both at the local (Horváth et al. 2019, Holmes et al. 2020) and the landscape scale (Horváth et al. 2019). This calls for a better understanding of connectivity within their remaining networks, both for conservation and efficient restoration measures. Graph-based measures can be important connectivity metrics to understand the functioning of habitat networks (Urban and Keitt 2001), and for such analyses, well-delineated networks of pools and ponds could provide ideal test cases. Surprisingly though, such explicit network analyses involving ponds are still scarce (exceptions include e.g. Thornhill et al. 2018, Godet and Clauzel 2021) including their utilisation for metacommunity theory in understanding drivers of biodiversity patterns (Borthagaray et al. 2015, Cunillera-Montcusí et al. 2021).

While there is an upsurge in studies focusing on the role of spatial configuration within pond networks in shaping the structure and dynamics of aquatic metacommunities, there is a significant knowledge gap in understanding the role of pond configuration in networks over smaller spatial scales (within a few km, where most of the dispersal events supposedly happen). Most of the previous works come from

networks over large distances, many times not capturing all ponds in the landscape (Soininen et al. 2007, Florencio et al. 2014, Gálvez et al. 2023). While these studies are very informative on distance-based community similarities and general community patterns, they cannot offer a full view of the functioning of the habitat network per se. A central-peripheral connectivity gradient in a pondscape might underlie the main biodiversity gradients, with central ponds hosting more species or playing a relatively more important role (Borthagaray et al. 2015, Cunillera-Montcusí et al. 2020, Holmes et al. 2020). However, these patterns are largely masked in such study designs and can only reliably be revealed in pondscapes if the entire network is considered for the calculation of network properties (i.e. measures of centrality).

In addition to spatial distances, the dispersal capacity of organisms among habitat patches also varies according to key traits such as dispersal mode and body size. Passive dispersers, for instance microscopic organisms, rely on dispersal vectors, such as wind or animals (Bilton et al. 2001, Mony et al. 2022). Their dispersal potential is expected to decrease with body or propagule size (De Bie et al. 2012). Active dispersers include organisms with life stages capable of vector-independent movement, such as amphibians or flying insects. As these groups can actively select suitable habitat patches, their distribution patterns are expected to be more determined by the local environmental conditions than passive dispersers of similar body size (Heino 2013). In contrast to passive dispersers, the dispersal ability of active dispersers is expected to increase with body size (Alzate and Onstein 2022, Cote et al. 2022). While small-bodied chironomids mostly stay within 200 m of their emergence site (Khan 2012), larger aquatic heteropterans disperse readily over 1.6 km (Briers 1998, Choi and Kim 2009), and most amphibian species cover distances up to a few kilometers (Smith and Green 2005).

Small passive dispersers and active, good dispersers are assumed to disperse well over large distances and thus their communities are not expected to show spatial patterns emerging from dispersal limitation across small spatial scales. Consequently, small scales stretching over only a few kilometers are often neglected in metacommunity studies. Nonetheless, studying community patterns at small spatial scales could still be informative: large passive dispersers may display spatial patterns across small scales due to low dispersal ability (Cottenie and De Meester 2003, Cottenie et al. 2003) and even active dispersers due to territorial behaviour (McCauley 2010) or differences in the surrounding matrix (Gall et al. 2017). Even so, recent studies tend to concentrate on a single or a limited number of organism groups, while multi-group studies, covering a wide range of taxonomic groups with diverse dispersal traits are still scarce, even though they have been increasing in recent years (Allen et al. 1999a, b, De Bie et al. 2012, De Marco et al. 2014, Gálvez et al. 2023). Such studies are crucial as they can corroborate the overall functioning of connectivity networks within aquatic networks by highlighting congruent patterns across diverse taxa.

The aim of the current study was to investigate how the relative position of ponds in a well-delineated pond network affects local taxonomic richness and metacommunity structure, i.e. the among-site variation in taxonomic composition of multiple organism groups, encompassing a variety of dispersal traits. As a model system, we used a cluster of closely-spaced bomb crater ponds, with over 50 habitats situated on a spatial scale of a few hundred meters. We specifically tested whether local taxonomic richness scales positively with the centrality of the ponds in a graph-based approach. In addition, we quantified the extent to which spatial configuration predicts metacommunity structure based on eigenvector analysis. We expected to detect spatial signals despite the small spatial extent, linked to the presumed higher dispersal rates among more central ponds, which should result in a gradient of biodiversity along the gradient of connectivity. Further, we also predicted that the strength of spatial signals will vary between organism groups linked to body size and dispersal mode as key traits. Specifically, we expected weaker spatial signals in the richness and community structure of taxa assumed to be good dispersers (i.e. especially for large active and small passive taxa) and stronger for groups more constrained due to larger size or lower motility.

## Material and methods

### Study area

A network of 112 bomb crater ponds forming a well-delineated pondscape relatively isolated from other waterbodies is situated in the Kiskunság area, central Hungary (Fig. 1). These ponds were likely created during World War II by mis-targeted bombing on a sodic meadow. They are saline waters mostly dominated by sodium carbonates and hydrocarbonates, and despite being the same age and in close proximity to each other, they vary in many of their environmental and morphological characteristics including hydroperiod, surface area, depth and vegetation cover (Vad et al. 2017, Supporting information). The ponds are not physically connected thus dispersal is expected to occur via wind, animal vectors or active movement of the organisms. The study area is located in a plain with negligible elevation change and no landscape feature that could potentially hinder dispersal (Fig. 1B), however, the rim of the ponds protrude as a consequence of the explosions. This prevents dispersal via waterways even when the meadows are wet but at low water levels, may also impede aerial and overland dispersal to some extent (Brans et al. 2023). The ponds are rarely visited by wading birds or other terrestrial animals making wind presumably the major dispersing force in the area for passive dispersers. We surveyed all ponds holding water in late spring (i.e. omitting the smallest and ephemeral habitats that were already dry at the time of the survey), resulting in a total of 54 ponds. The average distance between these ponds is 285 m and all habitats are situated within 1 km (min. and max. distances between the centre point of ponds: 9–863 m).

### Sample collection and environmental data

Fieldwork was carried out between 7 and 9 May 2014. A range of physical and chemical parameters was recorded on site including water depth (cm), diameter (m), open surface area (%), emergent and submerged vegetation (%). Conductivity ( $\text{mS cm}^{-1}$ ) and pH were measured using a field multimeter (Eutech CyberScan PCD 650). Per pond, a total of 10 l of water was collected and mixed from 10 randomly chosen points, of which 1 l was taken for water chemistry analysis and community sequencing of pro- and microeukaryotes. 1–50 ml (depending on turbidity) of this water sample was filtered through a nitrocellulose membrane filter ( $\text{\O} 47$  mm,  $0.22 \mu\text{m}$  pore size). These filters were stored at  $-20^\circ\text{C}$  until DNA extraction. Concentrations of total phosphorus (TP,  $\text{mg l}^{-1}$ ), total suspended solids (TSS,  $\text{mg l}^{-1}$ ), dissolved inorganic nitrogen (DIN,  $\text{mg l}^{-1}$ ), and chlorophyll *a* (Chl-*a*  $\mu\text{g l}^{-1}$ ) were measured in the lab as detailed in Vad et al. (2017). The concentration of  $\text{Ca}^{2+}$  was determined via complexometric titration (Eaton et al. 2005).

To collect zooplankton samples, 10 l of water was randomly collected from the open water and sieved through a  $45\text{-}\mu\text{m}$  mesh. Macroinvertebrates were sampled using sweep netting standardised to 3 min (frame-size:  $0.25 \times 0.25 \text{ m}^2$ , mesh size:  $500 \mu\text{m}$ ), for which all microhabitats present in a pond were included. Zooplankton and macroinvertebrate samples were preserved in 70% ethanol for further analysis. For the amphibian survey, hand netting maximised to 15 min, visual searches, and dip netting for tadpoles and newt larvae were applied. All identified specimens were released back to their habitat. For a more detailed description of the study area and sampling procedures, see Vad et al. (2017).

### Sample processing and community datasets

We focused on the following organism groups in our study (Supporting information): prokaryotes, phototrophic microeukaryotes, heterotrophic microeukaryotes, crustacean zooplankton (copepods and cladocerans), rotifer zooplankton, dipterans, other macroinvertebrates, and amphibians-reptilians. The isolation of community DNA from the membrane filters was carried out using the PowerSoil® DNA Isolation Kit (MO BIO Laboratories Inc.). Prokaryotic 16S and microeukaryotic 18S rRNA gene amplification and sequencing were performed by LGC Genomics (Berlin, Germany). For gene amplification, the following primer pairs were applied: EMBf 515F (GTGYCAGCMGCCGCGGTAA, Parada et al. 2016) – EMBr 806R (GGACTACNVGGGTWTCTAAT, Apprill et al. 2015) for the V4 region of the prokaryotic 16S rRNA gene and UnivF-1183mod (AATTTGACTCAACRCGGG) – UnivR-1443mod (GRGCATCACAGACCTG) (Ray et al. 2016) for the V7 region of the eukaryotic 18S rRNA gene. Sequencing was carried out on an Illumina MiSeq platform. For a detailed description of the entire procedure, see Szabó et al. (2022). Amplicon readsets were analysed using ‘mothur’ ver. 1.43.0 (Schloss et al. 2009) involving, sequence processing, taxonomic

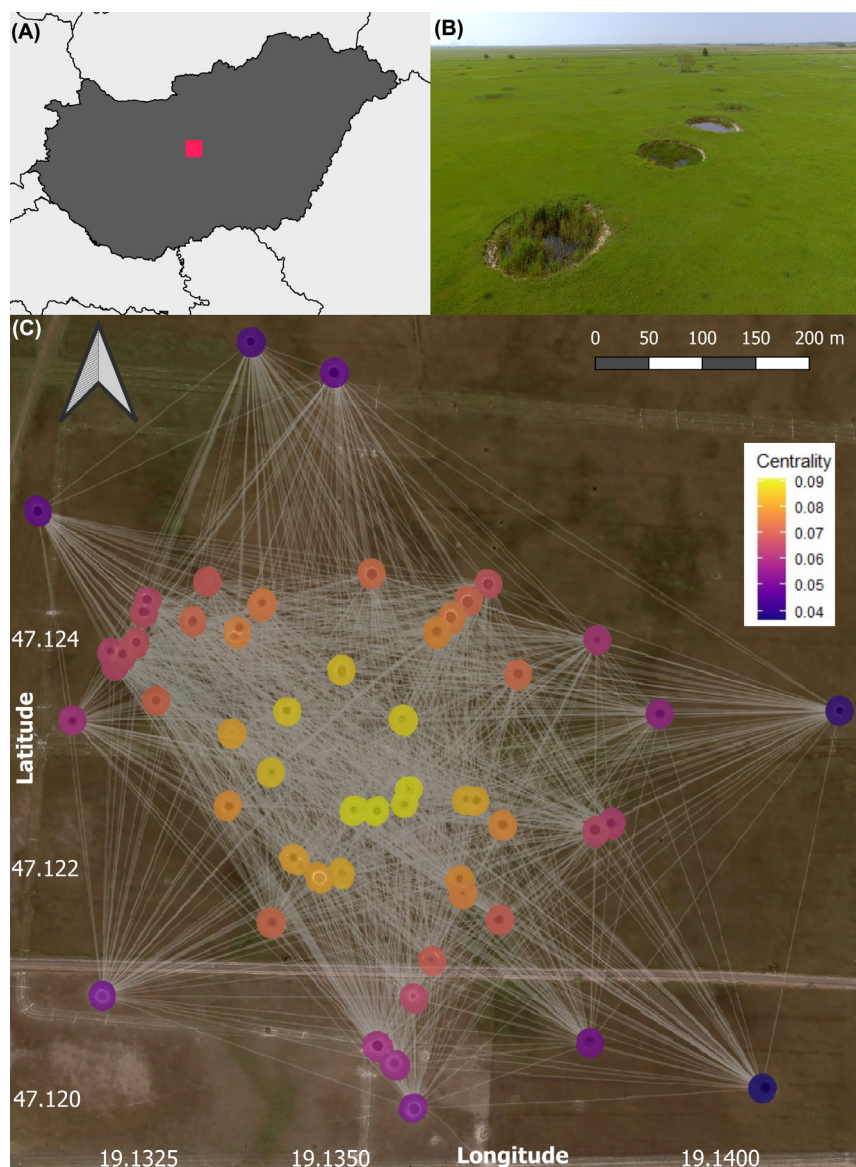


Figure 1. (A) Location of the study region near Apaj in Hungary. (B) Drone photo of a subset of the bomb crater pond network. (C) Location of the 54 bomb crater ponds with their closeness centrality scores indicated by a colour gradient (Google Earth Pro 2014, QGIS Development Team 2022).

assignments, and OTU picking with the MiSeq SOP as a reference ([www.mothur.org/wiki/MiSeq\\_SOP](http://www.mothur.org/wiki/MiSeq_SOP); Kozich et al. 2013, downloaded 12 November 2020). Additional quality filtering steps were implemented to minimize the presence of sequence artefacts. These steps included the adjustment of the deltaq parameter to 10 in the 'make.contigs' command, primer removal from both ends of the sequences, chimera identification and removal using the mothur-implemented version of VSEARCH and the exclusion of singleton reads. De-noising was carried out using mothur's 'pre.cluster' command with the suggested 2 bp difference cutoff. Read alignment and taxonomic assignment were performed using the ARB-SILVA SSU Ref NR 138 reference database with a minimum bootstrap confidence score of 80 (Quast et al. 2013). Non-primer-specific taxonomic

groups ('Chloroplast', 'Mitochondria' and 'unknown') were excluded from the dataset.

OTUs were selected at the 99% similarity threshold. Taxonomic assignment of 18S rRNA gene OTUs was performed using the 'classify.otu' command with the PR2 ver. 4.12.0 reference database (Guillou et al. 2012). 18S rRNA gene OTUs assigned to taxa Streptophyta, Metazoa, Ascomycota, and Basidiomycota were excluded from the microeukaryotic dataset. For the taxonomic assignment of prokaryotic OTUs, the TaxAss software (Rohwer et al. 2018) was used with default parameters and the FreshTrain (15 June 2020 release) and ARB-SILVA SSU Ref NR 138 databases. Subsequently, both 16S and 18S OTU sets were rarefied to the read number of the sample having the lowest sequence

count. Samples BC40 and BC105 were excluded from the eukaryotic dataset due to a low read count after filtering.

Zooplankton was identified to the lowest possible taxonomic level by microscopic analysis (generally to species), except for bdelloid rotifers which were treated as a single group. Macroinvertebrates were also identified to the lowest possible taxonomic level (generally to family, genus and species levels, depending on the higher taxa) using relevant identification keys (Supporting information). As passively dispersing macroinvertebrates were represented only by four taxa (Vad et al. 2017), they were excluded from the subsequent analyses. For a detailed description of the sample processing and the list of identified taxa, Vad et al. (2017).

For community matrices of prokaryotes and microeukaryotes, we used the rarified 16S and 18S OTU tables. The 18S dataset was split into phototrophs and heterotrophs based on phyla using the 'phyloseq' package ver. 1.36.0 (McMurdie and Holmes 2013) in R 4.1.0 (www.r-project.org). Phototrophs mostly included groups capable of photosynthesis, while heterotrophs consisted of the remaining groups (Supporting information). Dipterans were treated separately from other macroinvertebrates as they are considered weak active dispersers (Bilton et al. 2001, Heino 2013). Other macroinvertebrates (Supporting information) included all actively dispersing groups considered intermediate or strong aerial dispersers with flying adults according to Heino (2013).

## Statistical analysis

In order to assess the relative importance of environmental and spatial predictors in explaining patterns of taxonomic richness and community similarity, we carried out three sets of variance partitioning analyses using the *varpart* function of the 'vegan' package (Oksanen et al. 2020), where either network position (in the case of taxonomic richness) or spatial distance (in the case of taxonomic richness and community similarity) was included as the spatial predictor. We used data from all 54 ponds in all three cases, except for phototrophic and heterotrophic microeukaryotes for which data was available from 52 ponds only. In the environmental dataset, we excluded highly correlated (i.e. Pearson's  $r > 0.75$ ) environmental variables (turbidity, percentage of reed cover) prior to the analyses. Secchi depth and submerged vegetation cover were also excluded, as Secchi depth delivers very similar information as TSS but on a less precise scale, while the percentage of submerged vegetation cover almost exclusively contained zeros. Our final environmental dataset thus contained 10 variables, which were tested for normality and those deviating from it (Shapiro–Wilk test  $p < 0.05$ ) were transformed (conductivity, pH, depth – untransformed; DIN, TP, TSS – natural log;  $Ca^{2+}$ , surface area – square root; Chl-*a* –  $\log(x + 1)$ ; open surface area – cube transformed).

First, we analysed how taxonomic richness is predicted by the local environment and the relative position of ponds within the habitat network. For this, partial multiple linear regressions for each studied organism group were carried out using the *rda* function of the 'vegan' package (Oksanen et al.

2020). As a response variable, richness was included either as OTU (pro- and microeukaryotes) or taxonomic richness (other groups), but hereinafter, we refer to these as 'taxonomic richness' for simplicity. Richness as a count variable is generally recommended to be modelled using generalized linear models (GLM) with Poisson link. However, to be able to perform variance partitioning, we used linear models after transforming taxonomic richness data, if necessary, in order to achieve normal distribution. Taxonomic richness data were square-root transformed except for the active macroinvertebrate group. Model assumptions (normality, heterogeneity of variance) were visually checked (plotting residuals versus fitted values and normal Q–Q plots) and tested (Shapiro–Wilk test). No substantial deviations with regard to model assumptions were found. As environmental predictors, we used the first two axes of a principal component analysis (PCA) constructed for the environmental variables, following z-score standardisation. For all subsequent analyses, site scores of PC1 and PC2 axes (explaining  $> 65\%$  of the total variation, Supporting information) were extracted and used as environmental data. As a spatial predictor, we calculated the closeness centrality index of each pond (Fig. 1C) based on the spatial distance matrix of all ponds using the 'igraph', 'fields' and 'reshape2' packages (Csárdi and Nepusz 2006, Wickham 2007, Nychka et al. 2021). To test for the possible significance of the unique effects of environment and centrality, a permutation test (2000 permutations) was run for each partial multiple linear regression model using the function *anova*.

We run a second set of variance partitioning (partial multiple linear regression models) for each organism group separately to test if and how taxonomic richness is affected by the environmental variables (PC1 and PC2 axes) and the number of neighbouring ponds. In these models, environmental variables were included as one set of predictors the same way as described above, and the number of ponds within a radius with increasing distance from each local pond over a scale of 0–800 m, with 10 m increments was involved as the spatial predictor. The unique effects of space and environment were calculated the same way as in the first set of variance partitioning 80 times in total for each organism group. The unique effect of space along threshold distance (cut-off distance for calculating pond numbers) was plotted with the help of General Additive Models (GAMs, formula =  $y \sim s(x, k = 5)$ ) for each taxonomic group separately with the package 'ggplot2' (Wickham 2016).

Third, we tested how metacommunity structure is predicted by the local environment and spatial configuration of the ponds. Since we did not have abundance data for all organism groups, statistical analyses were run on presence–absence community data for comparability. Taxa occurring in less than three ponds were omitted given their minor contribution to the overall similarity in the community dataset. Then, any pond that contained no taxa was removed. Dissimilarity matrices were calculated based on Sørensen dissimilarity with the *vegdist* function of the 'vegan' package (Oksanen et al. 2020). Here, the initial pool of environmental predictors was

represented by the 10 transformed environmental predictors, while the spatial predictors were Moran's Eigenvector Maps (MEM). MEMs were constructed based on the spatial distance matrix using the *dbMEM* function of the 'adespatial' package (Dray et al. 2022) and only the 15 positive MEMs were retained (Bauman et al. 2018, Borcard et al. 2018, Supporting information). To select significant variables of each set of explanatory variables (environment and space), we applied stepwise selection both for the transformed environmental variables and for the positive MEM eigenvectors using the *ordstep* function (direction=both, perm.max=2000) of the 'vegan' package (Oksanen et al. 2020). These selection steps were done separately for each organism group resulting in different sets of retained environmental variables and MEMs (Supporting information). We carried out a set of partial distance-based redundancy analyses (dbRDA) using the *capscale* function of the 'vegan' package (Oksanen et al. 2020) followed by significance testing with a permutation test (2000 permutations) using the function *anova*.

All statistical analyses were carried out in R 4.1.0 ([www.r-project.org](http://www.r-project.org)) and figures were created using the 'ggplot2' (Wickham 2016), 'pubbr' (Kassambara 2020) and 'car' packages (Fox and Weisberg 2019).

## Results

### Taxonomic richness

Environment (represented by the first two PCA axes) was predominant in explaining variance in taxonomic richness in all organism groups (Fig. 2). The explained variance varied between 0 and 52.2% (Supporting information). The unique effect of relative spatial position (closeness centrality) was also relevant for several taxa with explained variance

varying between 0 and 10.6%. It was the highest in the case of rotifers, where it was comparable to the share of the environment. The relationship between taxonomic richness and centrality (with the environment partialled out) was positive in all the passive dispersers and the weakest active disperser dipterans (Supporting information).

With increasing radius size around the focal pond, the number of ponds within the radius increased rapidly until around 550 m where the curve saturates, indicating the most dense part of the pond cluster (Fig. 3A). Accordingly, the number of ponds above this distance did not explain a considerable amount of variance in taxonomic richness in any of the studied groups (Fig. 3B–D). At the same time, there was considerable variance in pond numbers within the scales of 150–550 m (Fig. 3A), with related spatial signals in the local taxonomic richness of four groups (prokaryotes, rotifers, crustacean zooplankton and dipterans Fig. 3B–D). Among the weakest disperser groups (large passive and small active dispersers, the relationship between pond number and taxonomic richness was strongest within a circle radius between 200 and 400 m for both zooplankton groups, while it was 300–700 m for dipterans. As the variation explained by the environment did not show a similar spatial structuring, this suggests that indeed neighbouring pond densities are the major driver of the observed pattern (Supporting information).

### Metacommunity structure

In metacommunity structure measured as community similarity, the overall pattern was similar to taxonomic richness with the environment explaining more variance than space in most organism groups (Fig. 4). The amount of unique variance explained by the environment varied between 10.1 and 36.4%. The unique effect of space varied between 0.7

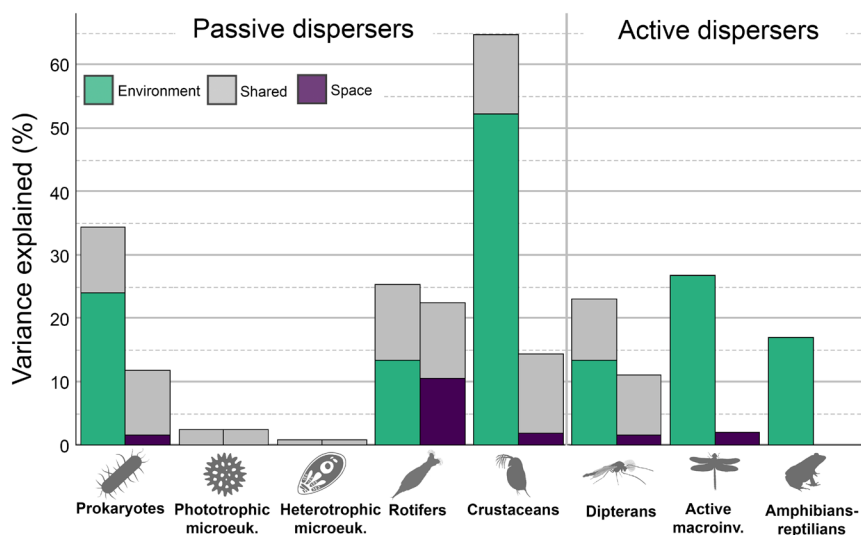


Figure 2. The variance of taxonomic richness explained by environment (PC1 and PC2 axes) and space (closeness centrality) of the studied organism groups of both passive and active dispersers, ordered according to body size within the two categories. The shared portion of the explained variance (grey shading) is shown at the top of the bars of both space and environment.

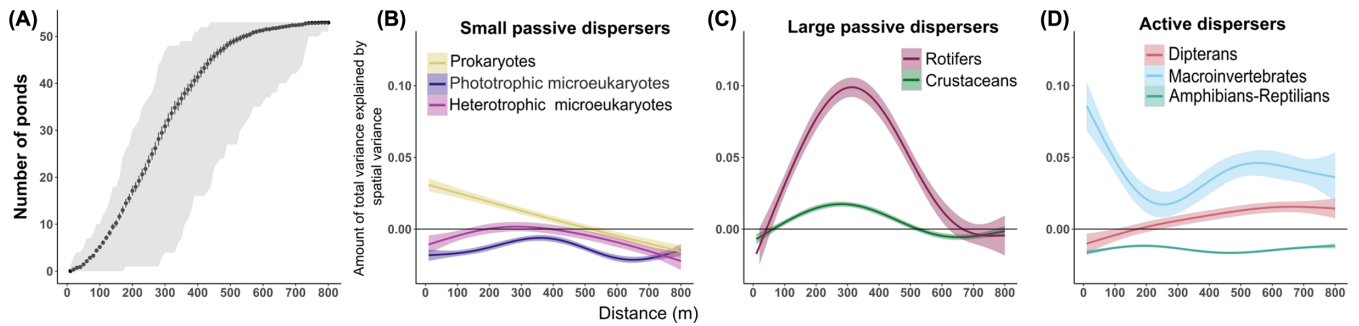


Figure 3. (A) The mean number of neighbouring ponds ( $\pm$  SE) around each pond within an increasing radius (cut-off distance), where grey shading shows the full range between minimum and maximum values. (B)–(D) Variograms with the amount of unique variance in taxonomic richness explained by the number of ponds within a radius against each cut-off distance partialling out the environmental variance (PC1 and PC2 axes).

and 15.6%, being the highest in rotifers and lowest in prokaryotes, respectively (Supporting information). In the case of rotifers, it even exceeded the unique share of variance explained by environment.

## Discussion

Our results highlighted the importance of connectivity for multiple organism groups in a delineated habitat network covering a small spatial scale of a few hundred metres. We found that pond taxonomic richness scales with network position and that spatial configuration has an imprint on metacommunity structure, i.e. the among-site variation in composition across multiple taxonomic groups. The local environment explained a larger share of the variance in both richness and metacommunity structure than space, indicating a predominant role of species sorting, which is not

surprising given the strong environmental gradients (e.g. salinity, vegetation cover). Despite this, we found a clear indication that space also played an important role in structuring the metacommunity of the bomb crater pond network with such a small spatial extent. This held for most of the studied organism groups and for both taxonomic richness and metacommunity structure. Overall, our results highlight the importance of dense habitat networks in sustaining biodiversity. Moreover, the various organism groups differed in the amount of variance explained in their richness and composition by space, and this could be linked to their dispersal abilities in line with our initial expectations.

While metacommunity processes are highly context-dependent, species sorting is expected to be predominant over small spatial scales, especially for microbes (De Bie et al. 2012, Hanly and Mittelbach 2017, Langenheder and Lindström 2019, Mony et al. 2022). In line with this, we found clear evidence for the predominance of species sorting for all

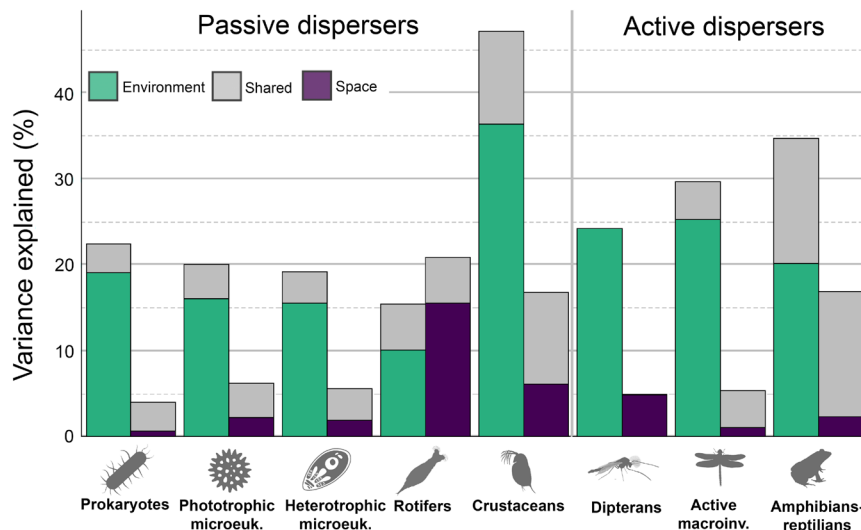


Figure 4. The proportion of unique variance explained by environment (selected environmental variables) and space (selected MEMs) in the community composition data of the various organism groups of both passive and active dispersers, ordered according to body size within the two categories. The shared portion of the explained variance (grey shading) is shown at the top of the bars of both space and environment.

organism groups, but with slightly different environmental variables being relevant for each group. Overall, conductivity, pH, and TSS were among the most important environmental predictors, which is in line with data from similar saline temporary waters from the region (Horváth et al. 2014, Horváth et al. 2016, Márton et al. 2023). However, while there was a strong environmental signal underlying community patterns, a significant spatial effect also emerged in multiple groups. These included the larger-bodied passively dispersing rotifer and crustacean zooplankton and the weak flyer dipterans, suggesting some level of dispersal limitation in their case.

The evidence for spatial structuring has been confirmed with complementary analyses, as we both explored the predictive role of relative spatial position (closeness centrality) for taxonomic richness and tracked community similarities based on spatial eigenvectors. The different sets of analyses gave consistent results, revealing the importance of spatial effects in the richness and metacommunity structure of the three organisms groups expected to be the weakest dispersers (i.e. large passive dispersers and weak active dispersers). For metacommunity structure, the first five MEM eigenvectors were the most frequently selected spatial explanatory variables across the organism groups. These correspond to the largest eigenvalues indicating coarse-scaled spatial structuring. Furthermore, multiple of these significant MEM eigenvectors (MEM 3, 4 and 5) illustrated the main spatial structuring between central and peripheral sites, similar to our results on centrality and richness. These overall indicated an important network effect in several organism groups, where richness is enhanced by a more central position of a local habitat via a higher number of surrounding patches, presumably related to the higher frequency of dispersal.

We expected to find more evidence for spatial structuring due to dispersal limitation in the weakest dispersing groups, large-bodied passive dispersers (rotifer and crustacean zooplankton) and the weak flyer dipterans. Our results were in line with this expectation as we found the largest positive spatial effects on taxonomic richness and largest spatial effects on community similarities in these three groups, being the most evident in rotifers. These patterns indicated some level of dispersal limitation at the spatial scale of our study. This finding aligns with previous studies that showed the importance of pond centrality for *Daphnia* metapopulation structure over a comparable spatial scale (Holmes et al. 2020) and the role of connectivity in structuring zooplankton metacommunities over larger scales of hundreds of square kilometers (Cottenie et al. 2003, Soininen et al. 2007). Contrary to these patterns, the taxonomic richness and community structure of prokaryotes and microeukaryotes showed only weak spatial structuring, which is in line with our expectations based on the findings of other studies on weak spatial patterns in prokaryotes across various spatial scales (Beisner et al. 2006, Van Der Gucht et al. 2007, De Bie et al. 2012, Padial et al. 2014). These taxa are easily dispersed by the wind even across vast distances (Smith et al. 2013, Mony et al. 2020) or via zoochory at small spatial scales (Lindström and Langenheder

2012, Szabó et al. 2022). Similarly, we found no or only weak evidence for spatial structuring in communities of actively flying macroinvertebrates (excluding dipterans), amphibians and reptilians. These groups are unlikely to show patterns related to dispersal limitation across such small scales due to their abilities to effectively cover distances larger than in our study system (Ficetola et al. 2004, Smith and Green 2005, Heino 2013, Florencio et al. 2014, Godet and Clauzel 2021).

Therefore, connectivity is an important determinant of biodiversity in pondscapes even across small spatial scales for at least some organism groups. The different groups of organisms that make up a metacommunity differ in their traits and the scales relevant to them in terms of spatial processes. Therefore, in multi-group studies, it is worth considering small spatial scales even if some groups are not expected to show spatial patterns. In several groups, the effect of connectivity was found to be more important when metacommunity structure was considered compared to taxonomic richness indicating that more connected patches do not necessarily hold more species but connectivity within the pondscape is an important determinant of metacommunity structure. Further analysis on more fine-scaled functional groups or at the level of species might even result in other spatial scales being important for certain groups of species.

There remains a large portion of unexplained variation in taxonomic richness and metacommunity structure for all groups, similar to other metacommunity studies (Soininen et al. 2007, Vanormelingen et al. 2008, De Bie et al. 2012). Our analyses were based on three complementary metrics of spatial configuration and an exhaustive dataset of the environmental variables making their effects less likely to be underestimated. At the same time, biotic interactions (competition, grazing, predation, mutualism, parasitism etc.) are likely to play a role in metacommunity structuring and may mask the effects of space or environment (Van De Meutter et al. 2008, Verreydt et al. 2012, Mony et al. 2022) and interspecific competition at the same trophic level can also affect spatial patterns (Thompson et al. 2020, Guzman et al. 2022). Finally, our study is only a snapshot in a presumably highly dynamic system and temporal aspects may need to be explored along with historical processes (Vyverman et al. 2007, Vanormelingen et al. 2008, Thompson et al. 2020, Guzman et al. 2022). Dormant eggs and other resting stages integrate past dispersal events and this could have masked recent dispersal events in passive dispersers in our study (Wisnoski et al. 2019, Holyoak et al. 2020, Wisnoski and Shoemaker 2022). Incorporating these effects in future studies would provide novel in-depth knowledge of the additional processes acting in such pondscapes, further increasing our understanding of how these habitat networks function.

In conclusion, we found that both space and environment shape the metacommunity of a pondscape even when the spatial extent is relatively small. Differences in spatial patterns between organism groups are likely attributable to group-specific differences in dispersal traits, with communities of actively dispersing larger animals and small passive dispersers



showing weak or no spatial signals. In contrast, communities of weak-disperser macroinvertebrates and especially large-bodied passive dispersers are structured by space to a greater extent. The fact that spatial patterns occur in metacommunity structure and central ponds in the network host higher richness highlights the importance of studying and protecting ponds as parts of a network. This needs to be taken into consideration during conservation planning to maximise the protection of overall biodiversity at both the local and landscape levels.

**Acknowledgements** – We acknowledge the work of Attila Péntek, Nastasia J. Cozma, Adrienn Tóth, Bence Tóth, Nóra A. Böde, Arnold Móra, and Katalin Zsuga who contributed to the original survey in the pondscape. Computations and data handling were enabled by resources of the ELTE Eötvös Loránd University. We are grateful for the insightful comments and suggestions provided by Jason Pither and an anonymous reviewer which greatly improved the manuscript. **Funding** – Barbara Barta is supported by ÚNKP-22-3 the New National Excellence Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund (ÚNKP-22-3-I-ELTE-568) and by NKFIH-K142296. Beáta Szabó and Zsófia Horváth acknowledge support by NKFIH-132095. Zsófia Horváth acknowledges support from the János Bolyai Research Scholarship of the Hungarian Academy of Sciences (grant no. BO/00392/20/8). Attila Szabó was supported by the Wenner-Gren Foundation. Zsófia Horváth and Csaba F. Vad acknowledge further support from the FWO project G0C3818N.

## Author contributions

**Barbara Barta:** Conceptualization (lead); Formal analysis (lead); Visualization (lead); Writing – original draft (lead). **Attila Szabó:** Data curation (equal); Methodology (supporting); Writing – review and editing (supporting). **Beáta Szabó:** Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (supporting); **Robert Ptacnik:** Funding acquisition (supporting); Resources (supporting); Writing – review and editing (supporting). **Csaba F. Vad:** Conceptualization (lead); Data curation (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Supervision (equal); Writing – original draft (lead). **Zsófia Horváth:** Conceptualization (lead); Data curation (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Supervision (equal); Writing – original draft (lead).

## Data availability statement

Data are available from Figshare: <https://doi.org/10.6084/m9.figshare.23867646.v1> (Barta et al. 2023) and raw sequence reads can be accessed at the NCBI SRA through BioProject ID PRJNA1005836.

## Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Allen, A. P., Whittier, T. R., Kaufmann, P. R., Larsen, D. P., O'Connor, R. J., Hughes, R. M., Stemberger, R. S., Dixit, S. S., Brinkhurst, R. O., Herlihy, A. T. and Paulsen, S. G. 1999a. Concordance of taxonomic richness patterns across multiple assemblages in lakes of the northeastern United States. – *Can. J. Fish. Aquat. Sci.* 56: 739–747.
- Allen, A. P., Whittier, T. R., Larsen, D. P., Kaufmann, P. R., O'Connor, R. J., Hughes, R. M., Stemberger, R. S., Dixit, S. S., Brinkhurst, R. O., Herlihy, A. T. and Paulsen, S. G. 1999b. Concordance of taxonomic composition patterns across multiple lake assemblages: effects of scale, body size, and land use. – *Can. J. Fish. Aquat. Sci.* 56: 2029–2040.
- Alzate, A. and Onstein, R. E. 2022. Understanding the relationship between dispersal and range size. – *Ecol. Lett.* 25: 2303–2323.
- Apprill, A., McNally, S., Parsons, R. and Weber, L. 2015. Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. – *Aquat. Microb. Ecol.* 75: 129–137.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M. and Turlure, C. 2013. Individual dispersal, landscape connectivity and ecological networks. – *Biol. Rev.* 88: 310–326.
- Barta, B., Horváth, Z., Vad, C., Ptacnik, R., Szabo, B. 2023. Data from: How pondscape function: Connectivity matters for biodiversity even across small spatial scales in aquatic metacommunities. Figshare. Dataset. – <https://doi.org/10.6084/m9.figshare.23867646.v1>
- Bauman, D., Drouet, T., Fortin, M. J. and Dray, S. 2018. Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. – *Ecology* 99: 2159–2166.
- Beisner, B. E., Peres-Neto, P. R., Lindström, E. S., Barnett, A. and Longhi, M. L. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. – *Ecology* 87: 2985–2991.
- Biggs, J., Corfield, A., Walker, D., Whitfield, M. and Williams, P. 1994. New approaches to the management of ponds. – *Br. Wildl.* 5: 273–287.
- Bilton, D. T., Freeland, J. R. and Okamura, B. 2001. Dispersal in freshwater invertebrates. – *Annu. Rev. Ecol. Syst.* 32: 159–181.
- Boothby, J. 1997. Pond conservation: towards a delineation of pondscape. – *Aquat. Conserv. Mar. Freshw. Ecosyst.* 7: 127–132.
- Borcard, D., Gillet, F. and Legendre, P. 2018. Spatial analysis of ecological data. – In: Borcard, D., Gillet, F. and Legendre, P. (eds), *Numerical ecology with R use R!* Springer International Publishing, pp. 299–367.
- Borthagaray, A. I., Berazategui, M. and Arim, M. 2015. Disentangling the effects of local and regional processes on biodiversity patterns through taxon-contingent metacommunity network analysis. – *Oikos* 124: 1383–1390.
- Brans, K. I., Vad, C. F., Horváth, Z., Santy, L., Cuypers, K., Ptacnik, R. and De Meester, L. 2023. Regional and fine-scale local adaptation in salinity tolerance in *Daphnia* inhabiting contrasting clusters of inland saline waters. – *bioRxiv*. Preprint, 11 August 2023, doi: <https://doi.org/10.1101/2023.08.11.552416>
- Briers, R. A. 1998. Metapopulation ecology of *Notonecta* in small ponds. – Univ. of Sheffield.
- Calabrese, J. M. and Fagan, W. F. 2004. A comparison-shopper's guide to Connectivity metrics. – *Front. Ecol. Environ.* 2: 529–536.
- Choi, H. and Kim, J. G. 2009. Landscape analysis of the effects of artificial lighting around wetland habitats on the giant water

- bug *Lethocerus deyrollei* in Jeju Island. – *J. Ecol. Field Biol.* 32: 83–86.
- Cote, J. et al. 2022. Dispersal syndromes in challenging environments: a cross-species experiment. – *Ecol. Lett.* 25: 2675–2687.
- Cottenie, K. and De Meester, L. 2003. Connectivity and cladoceran species richness in a metacommunity of shallow lakes. – *Freshw. Biol.* 48: 823–832.
- Cottenie, K., Michels, E., Nuytten, N. and De Meester, L. 2003. Zooplankton metacommunity structure: regional vs local processes in highly interconnected ponds. – *Ecology* 84: 991–1000.
- Csárdi, G. and Nepusz, T. 2006. The igraph software package for complex network research. – *InterJ. Complex Syst.* 1695: 1–9.
- Cunillera-Montcusí, D., Boix, D., Sala, J., Compte, J., Tornero, I., Quintana, X. D. and Gascón, S. 2020. Large- and small-regional-scale variables interact in the dispersal patterns of aquatic macroinvertebrates from temporary ponds. – *Aquat. Ecol.* 54: 1041–1058.
- Cunillera-Montcusí, D., Borthagaray, A. I., Boix, D., Gascón, S., Sala, J., Tornero, I., Quintana, X. D. and Arim, M. 2021. Metacommunity resilience against simulated gradients of wildfire: disturbance intensity and species dispersal ability determine landscape recover capacity. – *Ecography* 44: 1022–1034.
- De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W. and Declerck, S. A. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. – *Ecol. Lett.* 15: 740–747.
- De Marco, P., Nogueira, D. S., Correa, C. C., Vieira, T. B., Silva, K. D., Pinto, N. S., Bichsel, D., Hirota, A. S. V., Vieira, R. R. S., Carneiro, F. M., de Oliveira, A. A. B., Carvalho, P., Bastos, R. P., Ilg, C. and Oertli, B. 2014. Patterns in the organization of Cerrado pond biodiversity in Brazilian pasture landscapes. – *Hydrobiologia* 723: 87–101.
- Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Naima, M. and Wagner, H. H. 2022. *adespatial*: multivariate multiscale spatial analysis. R package version 0.3-16. – <https://CRAN.R-project.org/package=adespatial>.
- Eaton, A. D., Clesceri, L. S., Rice, E. W. and Greenberg, A. E. (eds) 2005. Standard methods for the examination of water and wastewater, 21st edn. – APHA, American Water Works Association, World Economic Forum.
- Ficetola, G. F., Padoa-Schioppa, E., Monti, A., Massa, R., Bernardi, F. D. De and Bottoni, L. 2004. The importance of aquatic and terrestrial habitat for the European pond turtle (*Emys orbicularis*): implications for conservation planning and management. – *Can. J. Zool.* 82: 1704–1712.
- Fletcher, R. J., Burrell, N. S., Reichert, B. E., Vasudev, D. and Austin, J. D. 2016. Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. – *Curr. Landsc. Ecol. Rep.* 1: 67–79.
- Florencio, M., Díaz-Paniagua, C., Gómez-Rodríguez, C. and Serano, L. 2014. Biodiversity patterns in a macroinvertebrate community of a temporary pond network. – *Insect Conserv. Divers.* 7: 4–21.
- Fox, J. and Weisberg, S. 2019. *An R Companion to applied regression*, 3rd edn. – Sage.
- Gall, M. L. Le, Chaput-Bardy, A. and Husté, A. 2017. Context-dependent local movements of the blue-tailed damselfly, *Ischnura elegans*: effects of pond characteristics and the landscape matrix. – *J. Insect Conserv.* 21: 243–256.
- Gálvez, Á., Peres-Neto, P. R., Castillo-Escrivà, A., Bonilla, F., Camacho, A., García-Roger, E. M., Iepure, S., Miralles-Lorenzo, J., Monrós, J. S., Olmo, C., Picazo, A., Rojo, C., Rueda, J., Sahuquillo, M., Sasa, M., Segura, M., Armengol, X. and Mesquita-Joanes, F. 2023. Inconsistent response of taxonomic groups to space and environment in Mediterranean and tropical pond metacommunities. – *Ecology* 104: e3835.
- Godet, C. and Clauzel, C. 2021. Comparison of landscape graph modelling methods for analysing pond network connectivity. – *Landsc. Ecol.* 36: 735–748.
- Google earth pro V 7.3.4.8642. 2014. Apaj bomb crater ponds, Hungary. 47°07'23.27"N, 19°08'13.35"E, Eye alt 1.38 km. – Image 2022 Maxar technologies.
- Guillou, L. et al. 2012. The Protist ribosomal Reference database (PR2): a catalog of unicellular eukaryote Small Sub-Unit rRNA sequences with curated taxonomy. – *Nucl. Acids Res.* 41: D597–D604.
- Guzman, L. M., Thompson, P. L., Viana, D. S., Vanschoenwinkel, B., Horváth, Z., Ptacnik, R., Jeliakov, A., Gascón, S., Lemmens, P., Anton-Pardo, M., Langenheder, S., De Meester, L. and Chase, J. M. 2022. Accounting for temporal change in multiple biodiversity patterns improves the inference of metacommunity processes. – *Ecology* 103: e3683.
- Hanly, P. J. and Mittelbach, G. G. 2017. The influence of dispersal on the realized trajectory of a pond metacommunity. – *Oikos* 126: 1269–1280.
- Heino, J. 2013. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? – *Oecologia* 171: 971–980.
- Holmes, C. J., Rapti, Z., Pantel, J. H., Schulz, K. L. and Cáceres, C. E. 2020. Patch centrality affects metapopulation dynamics in small freshwater ponds. – *Theor. Ecol.* 13: 435–448.
- Holyoak, M., Caspi, T. and Redosh, L. W. 2020. Integrating disturbance, seasonality, multi-year temporal dynamics, and dormancy into the dynamics and conservation of metacommunities. – *Front. Ecol. Evol.* 8: 571130.
- Horváth, Z., Vad, C. F., Tóth, A., Zsuga, K., Boros, E., Vörös, L. and Ptacnik, R. 2014. Opposing patterns of zooplankton diversity and functioning along a natural stress gradient: when the going gets tough, the tough get going. – *Oikos* 123: 461–471.
- Horváth, Z., Vad, C. F. and Ptacnik, R. 2016. Wind dispersal results in a gradient of dispersal limitation and environmental match among discrete aquatic habitats. – *Ecography* 39: 726–732.
- Horváth, Z., Ptacnik, R., Vad, C. F. and Chase, J. M. 2019. Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. – *Ecol. Lett.* 22: 1019–1027.
- Kassambara, A. 2020. *ggpubr*: “ggplot2” Based Publication Ready Plots. R package version 0.4.0. – <https://CRAN.R-project.org/package=ggpubr>.
- Khan, H. R. 2012. Effects of dispersal on community structure of aquatic insects in Arctic lakes and streams. – Umea Univ., Sweden.
- Kozich, J. J., Westcott, S. L., Baxter, N. T., Highlander, S. K. and Schloss, P. D. 2013. Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. – *Appl. Environ. Microbiol.* 79: 5112–5120.
- Langenheder, S. and Lindström, E. S. 2019. Factors influencing aquatic and terrestrial bacterial community assembly. – *Environ. Microbiol. Rep.* 11: 306–315.

- Leibold, M. A. and Chase, J. M. 2018. Metacommunity ecology, vol. 59. – Princeton Univ. Press.
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Lindström, E. S. and Langenheder, S. 2012. Local and regional factors influencing bacterial community assembly. – *Environ. Microbiol. Rep.* 4: 1–9.
- Martínez-Sanz, C., Cenzano, C. S. S., Fernández-Aláez, M. and García-Criado, F. 2012. Relative contribution of small mountain ponds to regional richness of littoral macroinvertebrates and the implications for conservation. – *Aquat. Conserv. Mar. Freshw. Ecosyst.* 22: 155–164.
- Márton, Z., Szabó, B., Vad, C. F., Pálffy, K. and Horváth, Z. 2023. Environmental changes associated with drying climate are expected to affect functional groups of pro- and microeukaryotes differently in temporary saline waters. – *Sci. Rep.* 13: 3243.
- McCauley, S. J. 2010. Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). – *Ecol. Entomol.* 35: 377–385.
- McMurdie, P. J. and Holmes, S. 2013. phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. – *PLoS One* 8: e61217.
- Mony, C., Vandenkoornhuysse, P., Bohannan, B. J. M., Peay, K. and Leibold, M. A. 2020. A landscape of opportunities for microbial ecology research. – *Front. Microbiol.* 11: 561427.
- Mony, C., Uroy, L., Khalfallah, F., Haddad, N. and Vandenkoornhuysse, P. 2022. Landscape connectivity for the invisibles. – *Ecography* 2022: e06041.
- Nychka, D., Furrer, R., Paige, J. and Sain, S. 2021. fields: tools for spatial data. R package version 13.3. – <https://github.com/dnychka/fieldsRPackage>.
- Oertli, B., Joye, D. A., Castella, E., Juge, R., Cambin, D. and Lachavanne, J.-B. 2002. Does size matter? The relationship between pond area and biodiversity. – *Biol. Conserv.* 104: 59–70.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. and Wagner, H. 2020. vegan: community ecology package R package version 2.5-7. – <https://CRAN.R-project.org/package=vegan>.
- Padial, A. A., Ceschin, F., Declerck, S. A. J., Meester, D. and Bonecker, L. 2014. Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. – *PLoS One* 9: 111227.
- Parada, A. E., Needham, D. M. and Fuhrman, J. A. 2016. Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. – *Environ. Microbiol.* 18: 1403–1414.
- Pereira, M., Segurado, P. and Neves, N. 2011. Using spatial network structure in landscape management and planning: A case study with pond turtles. – *Landsc. Urban Plan.* 100: 67–76.
- QGIS Development Team. 2022. QGIS Geographic Information System (ver. 3.26.0). – Open Source Geospatial Foundation Project.
- Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J. and Glöckner, F. O. 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. – *Nucl. Acids Res.* 41: D590–D596.
- Ray, J. L., Althammer, J., Skaar, K. S., Simonelli, P., Larsen, A., Stoecker, D., Sazhin, A., Ijaz, U. Z., Quince, C., Nejstgaard, J. C., Frischer, M., Pohnert, G. and Troedsson, C. 2016. Metabarcoding and metabolome analyses of copepod grazing reveal feeding preference and linkage to metabolite classes in dynamic microbial plankton communities. – *Mol. Ecol.* 25: 5585–5602.
- Rohwer, R. R., Hamilton, J. J., Newton, R. J. and McMahon, K. D. 2018. TaxAss: leveraging a custom freshwater database achieves fine-scale taxonomic resolution. – *mSphere* 3: e00327–e00318.
- Schloss, P. D., Westcott, S. L., Ryabin, T., Hall, J. R., Hartmann, M., Hollister, E. B., Lesniewski, R. A., Oakley, B. B., Parks, D. H., Robinson, C. J., Sahl, J. W., Stres, B., Thallinger, G. G., Van Horn, D. J. and Weber, C. F. 2009. Introducing Mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. – *Appl. Environ. Microbiol.* 75: 7537–7541.
- Smith, M. A. and Green, M. D. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? – *Ecography* 28: 110–128.
- Smith, D. J., Timonen, H. J., Jaffe, D. A., Griffin, D. W., Birmele, M. N., Perry, K. D., Ward, P. D. and Roberts, M. S. 2013. Intercontinental dispersal of bacteria and archaea by transpacific winds. – *Appl. Environ. Microbiol.* 79: 1134–1139.
- Soininen, J., Kokocinski, M., Estlander, S., Kotanen, J. and Heino, J. 2007. Neutrality, niches, and determinants of plankton metacommunity structure across boreal wetland ponds. – *Ecoscience* 14: 146–154.
- Szabó, B., Szabó, A., Vad, C. F., Boros, E., Lukić, D., Ptacnik, R., Márton, Z. and Horváth, Z. 2022. Microbial stowaways: waterbirds as dispersal vectors of aquatic pro- and microeukaryotic communities. – *J. Biogeogr.* 49: 1286–1298.
- Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G. 1999. Connectivity is a vital element of landscape structure. – *NCASI Tech. Bull.* 2: 534.
- Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., Viana, D. S. and Chase, J. M. 2020. A process-based metacommunity framework linking local and regional scale community ecology. – *Ecol. Lett.* 23: 1314–1329.
- Thornhill, I., Batty, L., Hewitt, M., Friberg, N. R. and Ledger, M. E. 2018. The application of graph theory and percolation analysis for assessing change in the spatial configuration of pond networks. – *Urban Ecosyst.* 21: 213–225.
- Urban, D. and Keitt, T. 2001. Landscape connectivity: a graph-theoretic perspective. – *Ecology* 82: 1205–1218.
- Vad, C. F., Péntek, A. L., Cozma, N. J., Földi, A., Tóth, A., Tóth, B., Böde, N. A., Móra, A., Ptacnik, R., Ács, É., Zsuga, K. and Horváth, Z. 2017. Wartime scars or reservoirs of biodiversity? The value of bomb crater ponds in aquatic conservation. – *Biol. Conserv.* 209: 253–262.
- Van De Meutter, F., Stoks, R. and De Meester, L. 2008. Size-selective dispersal of *Daphnia* resting eggs by backswimmers (*Notonecta maculata*). – *Biol. Lett.* 4: 494–496.
- Van Der Gucht, K., Cottenie, K., Muylaert, K., Vloemans, N., Cousin, S., Declerck, S., Jeppesen, E., Conde-Porcuna, J. M., Schwenk, K., Zwart, G., Degans, H., Vyverman, W. and De Meester, L. 2007. The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. – *Proc. Natl Acad. Sci. USA* 104: 20404–20409.
- Vanormelingen, P., Cottenie, K., Michels, E., Muylaert, K., Vyverman, W. and De Meester, L. 2008. The relative importance of dispersal and local processes in structuring phytoplankton communities in a set of highly interconnected ponds. – *Freshw. Biol.* 53: 2170–2183.

- Vanschoenwinkel, B., De Vries, C., Seaman, M. and Brendonck, L. 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. – *Oikos* 116: 1255–1266.
- Verreydt, D., De Meester, L., Decaestecker, E., Villena, M. J., Van Der Gucht, K., Vannormelingen, P., Vyverman, W. and Declerck, S. A. J. 2012. Dispersal-mediated trophic interactions can generate apparent patterns of dispersal limitation in aquatic metacommunities. – *Ecol. Lett.* 15: 218–226.
- Vyverman, W., Verleyen, E., Sabbe, K., Vanhoutte, K., Sterken, M., Hodgson, D. A., Mann, D. G., Juggins, S., Vijver, B. Van de, Jones, V., Flower, R., Roberts, D., Chepurinov, V. A., Kilroy, C., Vanormelingen, P. and Wever, A. De 2007. Historical processes constrain patterns in global diatom diversity. – *Ecology* 88: 1924–1931.
- Wickham, H. 2007. Reshaping data with the reshape package. – *J. Stat. Softw.* 21: 1–20.
- Wickham, H. 2016. *ggplot2: elegant graphics for data analysis.* – Springer-Verlag.
- Wisnoski, N. I., Leibold, M. A. and Lennon, J. T. 2019. Dormancy in metacommunities. – *Am. Nat.* 194: 135–151.
- Wisnoski, N. I. and Shoemaker, L. G. 2022. Seed banks alter metacommunity diversity: the interactive effects of competition, dispersal and dormancy. – *Ecol. Lett.* 25: 740–753.