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Wartime scars or reservoirs of biodiversity? The value of bomb crater ponds in aquatic conservation

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ABSTRACT

Considering the ongoing loss of aquatic habitats, anthropogenic ponds are gaining importance as substitute habitats. It is therefore important to assess their functioning in comparison to their natural precursors. Here we assess the biodiversity value of sodic bomb crater ponds by comparing their gamma diversity to that of natural reference habitats, astatic soda pans, and assess their importance on the landscape level by studying alpha and beta diversity. We studied aquatic organisms ranging from algae to vertebrates in a dense cluster of 54 sodic bomb crater ponds in Central Europe. Despite the overall small area of the pond cluster, gamma diversity was comparable to that found in surveys of natural habitats that encompassed much wider spatial and temporal scales. We also found a considerable number of species shared with reference habitats, indicating that these anthropogenic habitats function as important refuge sites for several species that are associated with the endangered soda pans. Moreover, we found a number of regionally or worldwide rare species. Among the components of beta diversity, species replacement dominated community assembly. Individual ponds contributed similarly to beta diversity in terms of replacement, being equally important for maintaining high gamma diversity and emphasising the role of the pond network rather than individual ponds. This pattern was seen in all studied groups. Bomb crater ponds therefore acted as important contributors to aquatic biodiversity. Considering the tremendous losses of ponds throughout Europe, anthropogenic ponds should be taken into consideration in nature conservation, especially when occurring in pond networks.

1. Introduction

Ponds are the most numerous representatives of inland standing waters (Downing et al., 2006). They host unique flora and fauna and contribute over-proportionally to regional biodiversity (De Meester et al., 2005; Oertli et al., 2005) and global biogeochemical cycles (Downing et al., 2008; Downing, 2010). Currently, there is a growing interest in pond ecology within community ecology and conservation biology (De Meester et al., 2005; Oertli et al., 2009), mostly due to the recent revelation and acknowledgement of their general ecological importance (Céréghino et al., 2014). Small waterbodies are especially vulnerable to climate change and habitat degradation (including pollution, fish stocking) due to their limited volume (Biggs et al., 2005; Brooks, 2009). The estimated loss of ponds in the 20th century exceeds 50% in many European countries, and it is even up to 90% in some regions mainly related to agricultural land drainage and urbanisation (Hassall, 2014; Wood et al., 2003). Recognising the drastic loss of ponds, restoration and reconstruction projects were recently implemented in several regions worldwide (Frisch and Green, 2007; Shulse et al., 2010; Williams et al., 2010). Ponds created for human purposes or as a side effect of various anthropogenic activities are widespread, and may act as important surrogate habitats for species of which the natural habitats have been lost. However, we generally lack information how anthropogenic freshwater habitats, including ponds, support biodiversity (Chester and Robson, 2013).

Conservation actions usually aim at maximising diversity either at the local (alpha) or at the landscape level (gamma diversity). Naturally, these two entities are inherently linked through community turnover among habitats (beta diversity), but beta diversity itself is rarely considered explicitly (Airoldi et al., 2008; McKnight et al., 2007; Socolar et al., 2016). Directly addressing beta diversity involves the analysis of spatial heterogeneity in addition to the link between local environment and community composition, hence such an approach helps identifying factors and processes maintaining diversity on the landscape level (Fairbanks et al., 2001; Margules and Pressey, 2000; McKnight et al., 2007). Detailed analyses of commu-

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nity turnover in space are predominantly done in terrestrial systems (although examples for aquatic systems also exist, e.g. Al-Shami et al., 2013; Maloufi et al., 2016). In context of the ongoing loss of aquatic habitats, the role of spatial heterogeneity and the explicit analysis of beta diversity represent a particular gap (Socolar et al., 2016). Beta diversity of small aquatic habitats such as ponds is generally considered to be high, serving as a frequent argument for the importance of their conservation (De Meester et al., 2005), but this is rarely taken into consideration in their practical conservation which relies on prioritizing individual habitats (Hill et al., 2016).

Different organism groups may display various levels of congruence in their regional distribution patterns. Their simultaneous consideration enables us to achieve a more holistic understanding on the assembly of communities and more efficient conservation planning (Paavola et al., 2003; Schouten et al., 2010). However, when it comes to ponds, most studies have surveyed them as habitats for amphibians (e.g. Beja and Alcazar, 2003; Knutson et al., 2004; Ruhí et al., 2012), macroinvertebrates (e.g. Becerra-Jurado et al., 2012; Céréghino et al., 2008; Wood et al., 2001) or plankton (e.g. De Bie et al., 2007; Gallego et al., 2012; Mimouni et al., 2015), while biodiversity studies simultaneously considering different organism groups are much rarer (exceptions include e.g. De Bie et al., 2012; De Marco et al., 2013; Lemmens et al., 2013).

We aim here to assess the biodiversity value of a peculiar type of anthropogenic habitat, bomb crater ponds. These habitats occur all over the world in areas affected by military activities in the past 100 years. In our study region, the Pannonian Plain in Central Europe, they form very dense clusters of habitat patches. They were created mainly by military exercises over the last 70 years or mistargeted bombings during World War II. Being considered wartime scars, many of these bomb crater ponds are currently subject to grassland rehabilitation measures (including filling most of them in). These measures are typically applied without a proper evaluation of their contemporary biodiversity. Due to their common origin, bomb crater ponds represent morphologically very similar habitats. Additionally, ponds within clusters were created at the same time and in restricted geographic regions, providing ideal model systems to study how anthropogenic ponds maintain biodiversity on a spatial scale of where most conservation efforts take place. In general, we know very little about their aquatic communities, and so far they have never been specifically addressed by regional-scale studies.

As a model system, we chose a confined area harbouring a dense cluster of bomb craters situated in Central Hungary (54 ponds within a 1 km scale). We sampled these habitats simultaneously for benthic diatoms, zooplankton, macroinvertebrates and amphibians. Our first aim is to quantify their entire species inventory at the landscape level (gamma diversity) and compare it to other natural habitats in the region. Second, we aim to investigate how the observed gamma diversity is maintained within the cluster of bomb crater ponds by studying alpha and beta diversity (along with its components), and identify their main environmental drivers. More specifically, we test whether the individual contribution of ponds to the total variation (i.e. beta diversity) is similar or some habitats are unique biodiversity hotspots and should have higher conservation priority. By targeting multiple organism groups, we will also investigate whether there is a congruence pattern in diversity among them.

2. Materials and methods

2.1. Study area

The Pannonian Plain in Central Europe is characterised by diverse aquatic habitats, including a variety of ponds and pools (Boven et al., 2008a; Lukács et al., 2013), and even regionally restricted unique habitats with high conservation value such as the astatic soda pans, which are inland saline waters (Boros et al., 2014; Horváth et al., 2013a). The Kiskunság region in Hungary is a central part of the Plain, located on the interfluve of two large rivers, Danube and Tisza. It encompasses a diverse array of both aquatic (shallow lakes, swamps, peat bogs, sodic marshes, soda pans, temporary pools etc.) and terrestrial habitats (wet and dry meadows, sandy and sodic grasslands, semi-arid sand dunes, steppes etc.). These altogether allow the existence of a unique flora and fauna, with a high number of rare and endemic species (Boven et al., 2008b; Kovács-Láng et al., 2008; Ladányi et al., 2015). Large parts of the region belong to the Kiskunság National Park and are parts of a UNESCO Biosphere reserve, while a number of aquatic habitats are listed under the Ramsar Convention, Natura 2000 or IBA sites.

A dense cluster of bomb crater ponds is situated in the northernmost part of the National Park (47°7.403′N 19°8.187′E), near to the village of Apaj, Central Hungary, consisting of 112 ponds within a 1 km scale (Fig. 1 and Appendix, Fig. A1). They were created at the same time by mistargeted bombing of the nearby airport during World War II. Being formed on a sodic meadow, they hold sodic water (i.e. dominated by sodium carbonates and hydrocarbonates, see Appendix, Fig. B1). Their diameter varies between 3 and 12 m. While all of them are temporary waters, some (N = 58) hold water only for a few weeks mainly in early spring, fed by snowmelt, or after heavy rains throughout the year. These ponds have a maximum depth of 40 cm and many of them are overgrown by vegetation of common reed (*Phragmites australis*) and sedges (predominantly *Bolboschoenus maritimus*). The deeper ones (which are still < 1 m deep) are astatic, usually drying out in summer and filling up during late autumn or winter (N = 54). These deeper ponds have a bottom mostly free of marsh plants and have higher salinity. Some of them are inhabited by the Pannonian endemic fairy shrimp, *Chirocephalus carnuntanus*, already indicating the importance of the area for temporary water biodiversity (Horváth and Vad, 2015).

Due to their sodic and temporary features, these ponds are comparable to the natural astatic soda pans, which we used as reference habitats for floral and faunal similarities. Soda pans are an inland saline habitat type with distribution restricted to the Pannonian Plain in Europe (Horváth et al., 2014). These habitats represent an important natural heritage by hosting unique flora and fauna (Stenger-Kovács and Lengyel, 2015; Tóth et al., 2014) and as feeding grounds for several endangered waterbird species (Horváth et al., 2013a,b). However, soda pans have higher surface to volume ratio, a larger share of open water surface (i.e. without macrophytes; Boros et al., 2014), and their ecology is strongly linked to waterbirds (Boros et al., 2008), which features also imply basic differences between them and the sodic bomb crater ponds, which are only very scarcely visited by waterbirds.

2.2. Sampling

Between 7 and 9 May 2014, we performed a sampling for multiple groups (benthic diatoms, zooplankton, macroinvertebrates and vertebrates) along with physico-chemical measurements. By early

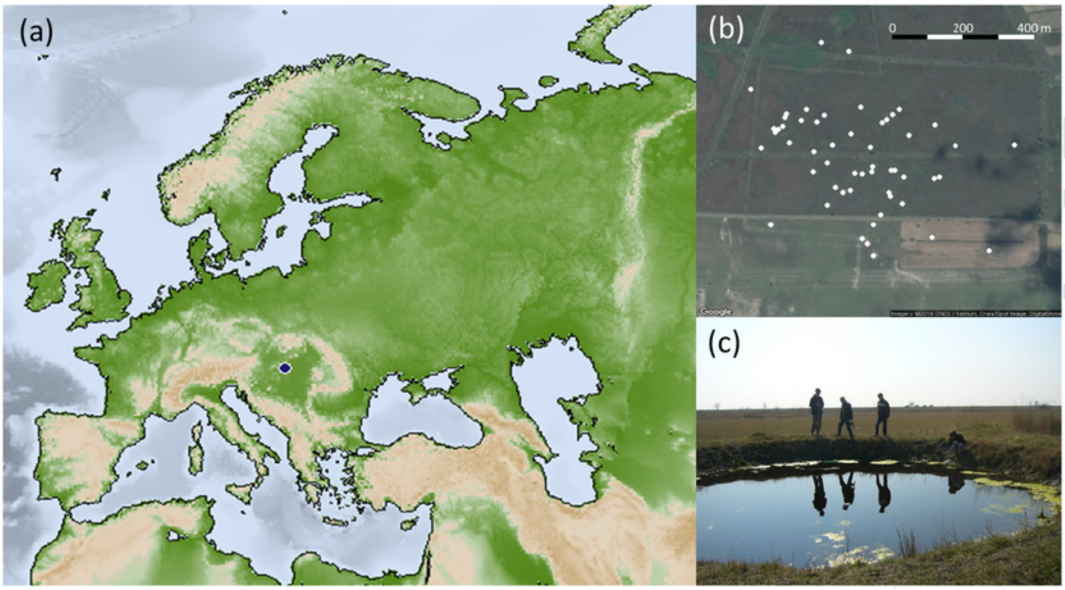

Fig. 1. The location of the study area in Europe (a) along with a map (b) and one example (c) of the habitats. On panel (b), the 54 ponds sampled within the study are indicated with filled white circles.

May, phytobenthos is already well-developed, and most macroinvertebrate and zooplankton species can generally also be found in late spring before summer desiccation. We sampled all habitats of the area, except for the ones with very short hydroperiod, which were already dry at this time of the year. This altogether resulted in 54 ponds.

Water depth, Secchi depth, and diameter of each pond, along with the percentages of open water surface and macrophyte coverage (submerged and emergent plants were considered separately) were recorded in situ. For measuring physico-chemical variables, we used a Eutech CyberScan PCD 650 field equipment for in situ determination of conductivity, pH and water temperature. Besides, water samples (1-litre subsample of a randomly collected 10-litre water sample) were taken for further laboratory analysis of total suspended solids, chlorophyll *a* and nutrient concentrations (total phosphorus, ammonium and nitrate concentrations).

Benthic diatom samples were primarily taken from green common reed (*Phragmites australis*) stems, or, if it was absent, from alkali bulrush (*Bolboschoenus maritimus*) or narrowleaf cattail (*Typha angustifolia*). Given the absence of vegetation in four ponds, samples were only collected from 50 ponds. We cut a 10-cm section of the stems starting at 10 cm below the water surface. Stems were chosen randomly in five replicates per pond.

For zooplankton samples, 10 l of water were randomly collected from the open water of each pond and sieved through a 45 μm mesh net thereafter. Separate samples were taken for rotifers and crustaceans. For macroinvertebrates, we applied sweep netting for three minutes per pond (frame-size: 0.25 × 0.25 m^2, mesh size: 500 μm), including all the microhabitats that were present in the ponds and the upper layer of the sediment. The samples were preserved in 70% ethanol.

For amphibians, 6 samplings were conducted during the breeding season (March–June), and another survey in September, including all 112 ponds of the area. These occasions were also used for recording any further presence of fairy shrimps. Hand netting supplemented by visual searching was used to record amphibians and dip netting for frog larvae and newts. In deeper and turbid waterbodies, hand netting time was maximised in 15 min. In smaller ones with high water transparency, < 15 min was considered to be representative. We were searching for amphibian larvae both in the centre and edge of the waterbodies, changing position in every minute. After identification, we released the captured specimens back into the ponds. We also recorded the presence of reptiles based on visual observation. Given the large difference between the gamma diversity of amphibians and reptiles compared to those of other groups and that fairy shrimps disappeared by May, data on amphibians, reptiles and fairy shrimps were only used for the species list of the area (Appendix, Table C2).

2.3. *Processing samples*

2.3.1. *Water analysis*

The concentration of total suspended solids (TSS) was determined gravimetrically by filtering water (2–50 ml, depending on turbidity) through pre-dried (oven-drying at 105 °C) and pre-weighted cellulose-nitrate membrane filters (pore size: 0.45 μm). Total phosphorous (TP) concentrations were measured spectrophotometrically as molybdate reactive phosphorous after persulphate digestion (Eaton et al., 2005). The concentrations of nitrate (NO_3-N) and ammonium (NH_4-N) were determined spectrophotometrically using the sodium salicylate method for NO_3-N (Scheiner, 1974) and the manual spectrometric method for NH_4-N (ISO, 1984). For chlorophyll analysis, a volume of 5–100 ml was filtered on glass-microfibre filters. Filters were stored frozen at − 20 °C. Chlorophyll *a* was eluated with methanol, boiled in a water bath for 2 min and measured spectrophotometrically after cooling (Sartory and Grobbelaar, 1984).

2.3.2. *Analysis of biological samples*

For analysing diatom samples, epiphyton was removed from the stems in the lab using different brushes and tap water and the samples were preserved with formaldehyde. Later on, they were treated with H_2O_2 and HCl (MSZ EN, 2014), washed five times with distilled water, and mounted with Naphrax® mounting medium. For identification, we used an Olympus IX70 inverted microscope equipped with differential interference contrast (DIC) optics at magnification of 1500 ×. At least 400 valves were counted and identified to species level per sample. For problematic taxa, a Zeiss EVO 10 scanning electron microscope was used for more precise identification. The treated samples were washed in distilled water, filtered through a 3 µm-mesh polycarbonate membrane, fixed on SEM stubs and coated with gold.

Depending on the densities, 10–20% of the zooplankton samples (achieved by subsampling of the total sample volume, 100 ml) were checked and all the observed specimens were identified to species level (usually at least 300 individuals for both rotifers and crustaceans) except for bdelloid rotifers that were treated as one single taxonomic group. We then checked the whole sample for rare species.

Among macroinvertebrates, coleopterans (except for some specific families/genera; Appendix, Table C1), heteropterans, odonates and chironomids were generally identified to species, while the other taxa (e.g. dipterans apart from chironomids) to genus or higher levels. In the analyses, we use the resulting number of taxa as “number of species”.

The taxonomic keys we used for the identification of each group are listed in Appendix B.

2.4. Data analysis

To present the general patterns in the environmental characteristics of the bomb crater ponds, we did a principal component analysis (PCA). As our variables had different scales, we performed the analysis on a correlation matrix with all variables being standardised to unit variance. Some environmental variables were transformed to normalise their distribution (details in Appendix, Fig. D1). PCA was performed with the ‘vegan’ package in R (Oksanen et al., 2013). A pairwise correlation plot of the environmental data is given in the Supplementary material (Appendix, Fig. D1).

In the species lists (Appendix Table C1 and C2), we present 111 macroinvertebrate taxa, but we use only 107 in the statistical analyses. We excluded Anostraca (2 species) as they were not observed during the main sampling when all other macroinvertebrates were collected. We also merged some Coleoptera and Heteroptera taxa, due to the high frequency of juveniles of congeneric species that could not be distinguished. The latter was carried out for large *Dytiscidae* spp. (adults were identified as *Cybister lateralimarginalis* and *Dytiscus circumflexus*) and the two *Notonecta* species (*Notonecta glauca* and *Notonecta viridis*).

To visualise the relationships between the mean alpha and observed gamma diversities of the three dominant groups (benthic diatoms, zooplankton, macroinvertebrates), we constructed species accumulation curves based on 999 random permutations with the ‘specaccum’ function of ‘vegan’ package in R (Oksanen et al., 2013).

To reveal the structure of gamma diversity in the three main groups, we partitioned it into relativised additive components, i.e. species replacement (Repl), richness difference (RichDiff) and similarity (Similarity) for all pairs of sites based on presence-absence data matrix. Here, Repl and RichDiff are the two components of beta diversity. Repl refers to the substitution of species among samples, while RichDiff indicates how much communities differ from each other in their number of species (Legendre, 2014). For this, we used the SDR-simplex approach (Podani and Schmera, 2011) based on Jaccard index. The pairwise values can then be presented on ternary plots (i.e. simplices) where Repl + RichDiff + Similarity = 1. With the pairwise sums of the additive components, it is also possible to compare the contribution of beta diversity (Repl + RichDiff) and nestedness (RichDiff + Similarity) to gamma diversity.

We then checked how individual ponds contribute to the species replacement and richness difference partitions of beta diversity. Legendre and De Cáceres (2013) proposed a method that allows calculating the local contribution to beta diversity (LCBD), in other words, the taxonomic uniqueness of individual sites in a region. The idea behind is that beta diversity can be measured as the total variation of a species by site community matrix and can be partitioned into species or local (i.e. site) contributions to beta diversity. LCBD can further be split into components, the local contributions of replacement and richness difference to total beta diversity (we will refer to this components as $\mathrm{Repl}_{\mathrm{LCBD}}$ and $\mathrm{RichDiff}_{\mathrm{LCBD}}$ throughout the text) can be calculated (Legendre, 2014).

To identify the primary predictors of alpha and beta diversity, we regressed local species richness (i.e. number of species) as a measure of alpha diversity, LBCD, and the two components of LCBD ($\mathrm{Repl}_{\mathrm{LCBD}}$ and $\mathrm{RichDiff}_{\mathrm{LCBD}}$) against the available suite of environmental gradients. Since some environmental predictors turned out to be highly collinear (Fig. 2; Appendix, Fig. D1), we performed an a priori data reduction by removing correlating variables based on pairwise Pearson's correlations (removing variables with r values larger than 0.6). We retained conductivity, TP, water depth, total surface area, and a proxy for dissolved inorganic nitrogen (DIN; derived from the summarized concentrations of NO_3-N and NH_4-N) in our initial set of explanatory variables. Initial analysis indicated non-linear relationships between some dependent and independent variables. Therefore we performed multiple linear regression using generalized additive models (GAMs) that allow fitting curvilinear relationships by smooth regression splines (Wood, 2011). Explanatory variables were then sequentially removed until only significant ones were retained in the final model ($p < 0.05$). We applied data transformations for macroinvertebrate LCBD and diatom, zooplankton and macroinvertebrate $\mathrm{RichDiff}_{\mathrm{LCBD}}$ (negative reciprocal transformation), macroinvertebrate $\mathrm{Repl}_{\mathrm{LCBD}}$ (square transformation), zooplankton LCBD and zooplankton and diatom species richness (ln transformation) to normalise model residuals. Among environmental predictors, TP and DIN were log-transformed. For an additional support for the

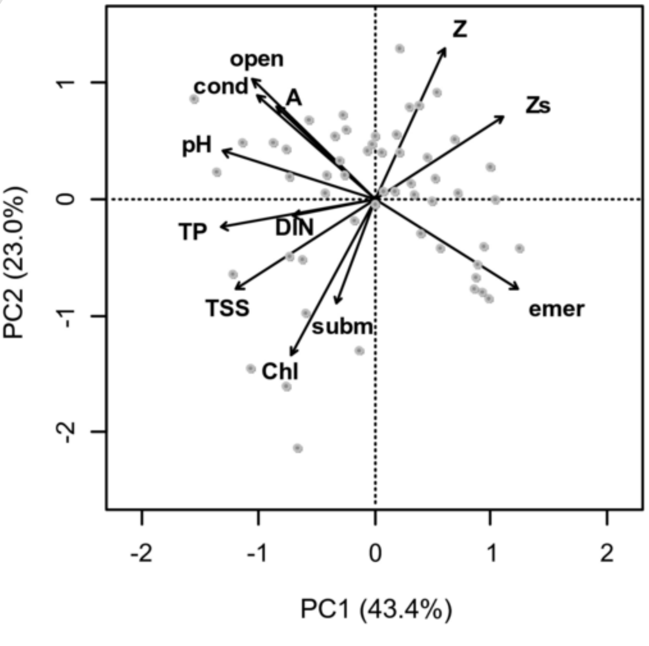

Fig. 2. PCA biplot for the recorded environmental variables and the sampling sites. Abbreviations: cond – conductivity, Z – depth, Z_S – Secchi depth, Chl – chlorophyll *a*, TSS – total suspended solids, Turb – turbidity, DIN – dissolved inorganic nitrogen, TP – total phosphorus, A – total surface area, open –open water surface, emer – emergent macrophyte coverage, subm – submerged macrophyte coverage.

role of environment, we ran the same analyses but this time using the first three axes (accounting for 76% of the total variation) of the PCA constructed for all measured environmental variables (see details on PCA above). GAMs were built with the 'mgcv' package of R (Wood, 2011).

3. Results

The investigated bomb crater ponds exhibited considerable variation in their physico-chemical environment (Table 1, Fig. 2). Conductivity correlated positively with pond size, pH and open water surface (i.e. less covered by macrophytes; Appendix Fig. D1). These were also grouped as one major group of environmental gradients on the PCA (Fig. 2). The second group of collinear variables comprised total suspended solids, chlorophyll *a* and water depth (the latter inversely correlated with the first two variables). Total phosphorus was situated in-between these two gradients on the PCA.

Altogether, we recorded 80 diatom, 74 zooplankton (48 rotifer, 26 crustacean), 111 macroinvertebrate and 9 vertebrate taxa. Among them, we found a number of halophilic specialists that were so far only reported from soda pans in the region, along with some rare and potentially threatened species (Table 2). A comparison of gamma diversities with that of the natural reference habitats (soda pans) revealed 45% of shared taxa in diatoms, 30% in zooplankton, 22–86% in macroinvertebrates and 100% in vertebrates. These comparisons along with species with the highest conservation values are summarized in Table 2, while a complete taxa list is provided in Appendix (Table C1).

Local species richness ranged between 0–30 (diatoms), 3–23 (zooplankton) and 1–32 (macroinvertebrates). The observed gamma diversities were 6.0 (diatoms), 7.6 (zooplankton) and 5.6 (macroinvertebrates) times higher than the average alpha diversities (mean ± SD for diatoms: 13.4 ± 4.9, zooplankton: 9.7 ± 4.8, macroinvertebrates: 19.2 ± 6.6; Fig. 3). Beta diversity was mostly driven by Repl rather than by RichDiff in all three groups (Fig. 4). Relativised beta diversity (sum of Repl and RichDiff; diatoms: 62.0%, zooplankton: 75.4%, macroinvertebrates: 72.3%) was also higher than nestedness (sum of RichDiff and Similarity; diatoms: 59.9%, zooplankton: 54.7%, macroinvertebrates: 53.9%).

$\text{RichDiff}_{\text{LCBD}}$ showed a right-skewed pattern according to the distribution frequency of calculated values, meaning that only a limited number of species-poor or species-rich sites occurred that contributed overproportionally to beta-diversity. In contrast, $\text{Repl}_{\text{LCBD}}$ showed a rather symmetric distribution frequency, which means that the majority of habitats contributed similarly to species replacement among the sites (Fig. 5, maps are presented in Appendix, Fig. E1). This pattern was very consistent among the three major groups, and was the most pronounced for macroinvertebrates (where $\text{Repl}_{\text{LCBD}}$ showed left-skewed distribution, implying an even larger difference between the relative importances of the two beta diversity components).

Table 1
Ranges, mean and median values of the environmental variables recorded for the 54 investigated bomb crater ponds.

	Min	Max	Mean ± SE	Median
Area (m^2)	7.1	113.0	45.2 ± 3.0	38.5
Depth (cm)	4.0	60.0	34.6 ± 2.0	35.5
Conductivity ($mS\ cm^{-1}$)	1.3	7.1	3.4 ± 0.2	3.4
pH	7.8	9.4	8.5 ± 0.0	8.4
Secchi-depth (cm)	2.0	50.0	17.4 ± 1.4	18.0
Total suspended solids ($mg\ l^{-1}$)	6.8	1390.0	113.6 ± 28.5	51.7
Total phosphorus ($mg\ l^{-1}$)	0.0	1.7	0.7 ± 0.1	0.5
Chlorophyll *a* ($\mu g\ l^{-1}$)	0.0	387.6	33.2 ± 9.6	10.5
Dissolved inorganic nitrogen ($mg\ l^{-1}$)	0.2	3.7	0.3 ± 0.0	0.3
Open water surface (%)	15.0	100.0	85.4 ± 2.4	94.0
Submerged macrophyte coverage (%)	0.0	20.0	0.7 ± 0.5	0.0
Emergent macrophyte coverage (%)	0.0	85.0	13.7 ± 2.4	6.0

Among environmental variables, TP was the only significant driver of diatom species richness, while zooplankton and macroinvertebrate species richness responded to more environmental gradients (Table 3). Among the predictors of LCBD, conductivity was significant in all three organism groups, along with TP (diatoms) and water depth (zooplankton and macroinvertebrates). Regarding $\text{Repl}_{\text{LCBD}}$, conductivity was significant for diatoms and area for macroinvertebrates, while in $\text{RichDiff}_{\text{LCBD}}$, TP for diatoms and conductivity for zooplankton. We did not find significant explanatory variables for zooplankton $\text{Repl}_{\text{LCBD}}$ and macroinvertebrate $\text{RichDiff}_{\text{LCBD}}$. Generally, alpha diversity and LCBD was best explained by the environmental parameters (R^2 adjusted ranged between 0.33–0.48 and 0.36–0.43). The components of LCBD, $\text{Repl}_{\text{LCBD}}$ and $\text{RichDiff}_{\text{LCBD}}$ could be explained less efficiently (Table 3). These patterns were very similar in the analyses with PCA axes as explanatory variables (Appendix, Table F1).

4. Discussion

Despite its small size, the cluster of bomb crater ponds studied here harboured a high biological diversity. For several taxa addressed in this survey, gamma diversity was comparable to that seen in natural reference habitats in the region. Moreover, some rare or endangered species were identified in every group (diatoms, zooplankton, macroinvertebrates, and vertebrates). Our analyses provide evidence for the primary importance of the whole pond network, rather than that of individual 'high-priority' ponds for the maintenance of gamma diversity. This is supported by the fact that species replacement was the dominant pattern of community assembly, and the contribution of replacement to total beta diversity was similar among the individual ponds in the network. These patterns generally hold for all three investigated organism groups.

When it comes to the assessment of the biodiversity value of anthropogenic habitats, it necessarily raises the question how important they are as refuge compared to natural habitats or as surrogate habitats when similar natural habitats are already lost (Chester and Robson, 2013). The species composition of the bomb crater ponds showed strong similarities to the flora and fauna of their reference habitats, soda pans, with a considerable number of shared species (Table 2). Especially interesting are the halophilic taxa that were previously only reported from soda pans in the region. Soda pans are the only natural saline waters in Central Europe, and they suffered serious decline in their numbers since the 18th century. Habitat loss is estimated to be 80% in Kiskunság (Horváth et al., 2013b), the region where the studied bomb crater ponds occur. Moreover, we found several specialists of temporary waters – habitats that are also disappearing at an alarming rate in most parts of the world (Jeffries et al., 2016; Zacharias and Zamparas, 2010). Considering this, the bomb craters represent a valuable refuge for halophilic and temporary water species along with halotolerant taxa comprising the communities of soda pans in general. The bomb crater ponds studied here act as surrogate habitats for several species associated with both soda pans and temporary freshwater habitats. This is also supported by the presence of flagship groups of temporary waters like fairy shrimps (Belk, 1998; Gascón et al., 2012), and the high diversity of amphibian species (most of them showing decreasing trends in their distribution; IUCN, 2016).

During the last 70 years since their origin, the bomb craters developed some gradients in the local environmental factors. They dis-

Table 2
Number of species found in the bomb crater ponds and in reference habitats. Overlap stands for the ratio of species shared with the species set of reference sites, except for Coleoptera, where we compared the overlap in genera due to differences in the taxonomic resolution (indicated with an asterisk). Only taxonomic groups with multiple species are included. References cited in the table are as follows: [1]Stenger-Kovács and Lengyel, 2015; [2]Levkov, 2009; [3]Hofmann et al., 2011; [4]Tóth et al., 2014; [5]Fontaneto et al., 2006; [6]Horváth et al., 2013b; [7]Eder and Hödl, 2002; [8]Gołdyn et al., 2012; [9]Horváth and Vad, 2015; [10]Boven et al., 2008b; [11]Forró, 2000; [12]Petri et al., 2012; [13]Csabai et al., 2002; [14]Cozma et al., 2014; [15]Csarmann, 2008; [16]IUCN, 2016; [17]Boros and Horváth, 2013.

Target group	Nr. of species (this study)	Nr. of species (reference habitats)	Overlap	Description of the reference study	Notable species	Description
Diatoms	80	188	45% (42 out of 93)	Long-term, large-scale survey with 210 samples from 31 soda pans in Austria and Hungary, listing the most typical 93 species of soda pans[1]	*Halamphora dominici*	Worldwide rare, halophilic, found only in a chilean salt lake and in soda pans of Central Europe[1,2]
					Halamphora paravenata, H. subcapitata, Hantzschia abundans	Halophilic, only occur in soda pans in Central Europe[1]
					Caloneis schumanniana, Gyrosigma acuminatum	Declining distributions according to the European Red list[3]
					Surirella brightwelli, Gomphonema jadwigiae	First findings in Hungary; *S. brightwelli* is halophilic[3]
Zooplankton	74	148	30% (45 out of 148)	All 110 soda pans in Central Europe[4]	*Arctodiaptomus spinosus*	Natronophilic, indicator species of soda pans[4]
					Brachionus asplanchnoides, Lecane lamellata, Hexarthra fennica	Halophilic, occurring exclusively in saline waters
Macroinvertebrates						
Anostraca	2	3	33% (1 out of 3)	Ninety-one soda pans in Central Europe[6]	*Chirocephalus carnuntanus, Eubranchipus grubii*	Both can be considered 'near threatened' or 'vulnerable' based on IUCN criteria[7,8]; *C. carnuntanus* is Pannonian endemic[9]; *E. grubii* was only reported twice in the last 25 years in Hungary[10,11]
Coleoptera	52	61	86% (26 out of 30)*	Eighteen soda pans and large sodic marshes, in a four-year study with a much higher spatial extent[12]	*Enochrus hamifer*	Halophilic, almost exclusively occurring in saline waters[13]
Odonata	6	27	22% (6 out of 27)		*Lestes dryas*	Protected by law in Hungary
Heteroptera	14	26	54% (14 out of 26)	Seasonal samples from 29 soda pans and sodic habitats between 1997 and 2010[14]		
Chironomidae	23	Unknown	Unknown	No comparable studies		
Vertebrates						All amphibians and reptiles are protected by law in Hungary
Amphibia	7	7	100% (7 out of 7)	Seasonal study of 35 soda pans and marshes in Austria[15]	*Triturus dobrogicus*	'Near threatened' with decreasing population trend[16]; reproduction observed in the bomb craters
					Bombina bombina, *Hyla arborea*, *Pelobates fuscus*, *Pelophylax esculentus complex*	Reproduction observed in the bomb craters; *B. bombina*, *H. arborea* and *P. fuscus* show decreasing population trends[16]
Reptilia	2	2	100% (2 out of 2)	All soda pans in Central Europe[17]	*Emys orbicularis*	'Near threatened'[16]; reproduction observed in the bomb craters

played salinities from sub- to hyposaline values (Hammer, 1986). Concentrations of total phosphorous and chlorophyll *a* ranged from oligotrophic to hypertrophic conditions. Some ponds were completely void of aquatic macrophytes, others were fully overgrown and there was an approximately 16 times difference between the area of the smallest and biggest habitats. Both TP (an indicator of trophic status) and conductivity were important predictors of species richness and LCBD. However, the directions of these relationships were different within the groups. For example, diatom species richness scaled negatively with TP, while the relationship between diatom LCBD and TP was positive. Similarly, in zooplankton and macroinvertebrates, conductivity showed a negative relationship with species richness, while its relationship with LCBD was U-shaped - meaning that the most unique communities were situated towards the two ends of the gradient. This has an important message for conservation, namely that the richest ponds do not necessarily host the most unique communities. This is also supported by examples on other systems and taxonomic groups (da Silva and Hernández, 2015; Heino and Grönroos, 2017; Legendre and De Cáceres, 2013; Mimouni et al., 2015; Qiao et al., 2015), while at the same time, this is not an obligatory pattern (Legendre and De Cáceres, 2013).

While species richness and LCBD showed relatively strong relationships with the environment, the total explained variance for $\text{Repl}_{\text{LCBD}}$ was limited. At the same time, species replacement was the dominant component of gamma diversity. According to Legendre (2014), species replacement predominantly implies the role of environmental filtering, competition or historical effects. As even with the rather exhaustive list of environmental variables we recorded, only a limited amount of the variation in $\text{Repl}_{\text{LCBD}}$ could be explained, this suggest that processes other than environmental filtering may act to maintain gradual replacement of species among ponds in the area. Although heterogeneity among local communities may arise

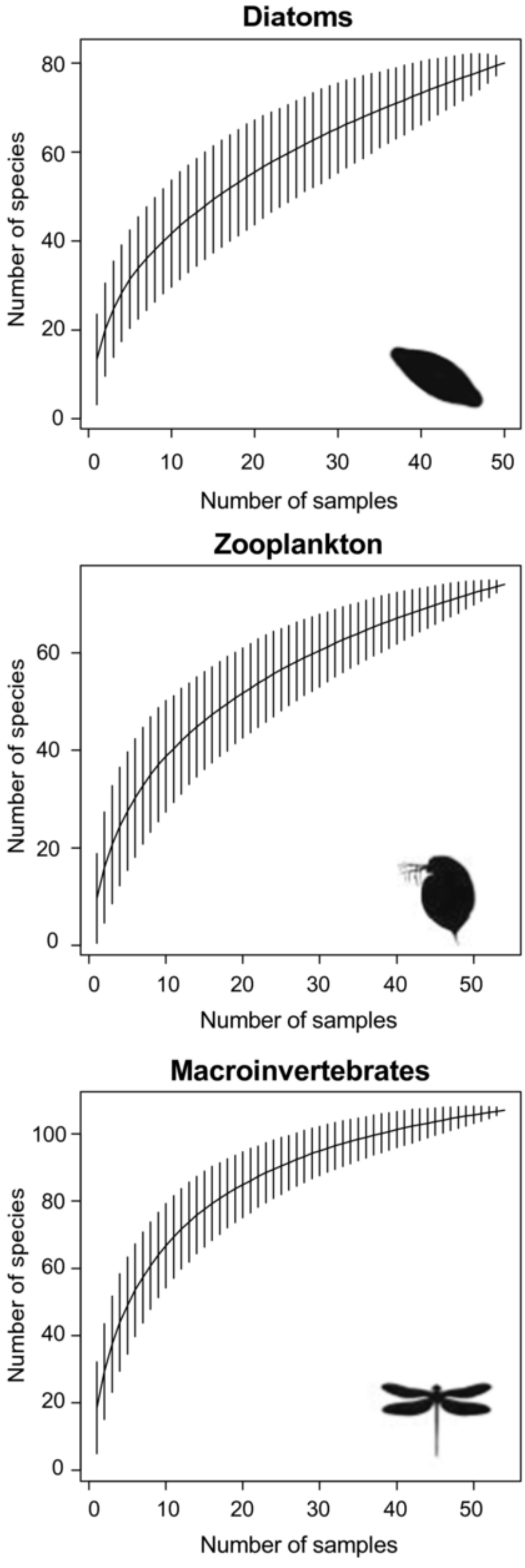

Fig. 3. Species accumulation curves constructed for benthic diatoms, zooplankton (Cladocera, Copepoda, Rotifera) and macroinvertebrates (Coleoptera, Heteroptera, Odonata, Chironomidae). Each sample refers to one pond.

from seasonal differences among habitats, the very limited spatial scale rules out of the relevance of climatic gradients. Asynchronous seasonal forcing should be especially unlikely among most macroinvertebrates, e.g. in aquatic insects that were represented by 107 out of 111 taxa in our data set. In their case, re-colonization cannot happen locally from the egg bank (unlike in plankton, where differences among local hatching cues might add to asynchrony on the regional level). As there were no systematic differences among these groups, seasonality as the primary driver can be refuted. Similarly to $\mathrm{Repl}_{\mathrm{LCBD}}$, $\mathrm{RichDiff}_{\mathrm{LCBD}}$ can to some extent also reflect environmental gradients, especially if there is a substantial community thinning along a certain gradient (Legendre, 2014). Interestingly, even though the significant explanatory factors of species replacement in the three organism groups resembled the ones for species richness, they did not explain a similarly high proportion of variation.

The three organism groups under study exhibited similar regional patterns with the overall dominance of species replacement. Diatoms, however, proved to be overall more similar than zooplankton and macroinvertebrates. When identifying the main drivers of alpha and beta diversity, diatoms seemed to be more strongly driven by TP (an indicator of trophic status) than the other two groups, as it was a significant driver of both diatom species richness, LCBD (together with conductivity) and $\mathrm{RichDiff}_{\mathrm{LCBD}}$. Their $\mathrm{Repl}_{\mathrm{LCBD}}$, however, was driven solely by conductivity. This overall suggests that total phosphorus mainly affects their richness while conductivity drives the gradual replacement of species (we however acknowledge that we cannot exclude the effect of some collinear variables not used in the analyses, e.g. TP was highly correlated with pH and the amount of total suspended solids; Appendix, Fig. D1). Macroinvertebrates and zooplankton proved to be more similar to each other in respect to the significant effect of conductivity on both richness and LCBD in the two groups. Congruency among aquatic taxa is generally low when considering cross-taxa correlations in alpha or beta diversity, for which the most often considered explanation is their differential response to environmental conditions (Heino, 2010). Our study gives an example for these responses: altogether, we found that the groups were most congruent in the response to environmental gradients in LCBD, less in species richness, while almost no similarities were found among the significant predictors of either LCBD component.

Beta diversity of ponds is often higher than that of other waterbodies (Davies et al., 2008; Williams et al., 2004). However, studies hitherto focusing on beta diversity of ponds were performed on much larger spatial scales; moreover, they did not quantify how the individual ponds contributed to the overall variability in community composition. In this study, we assembled a dataset on one specific type of ponds, occurring in a confined region, where catchment-level differences (e.g. human disturbance, differences in the regional species set, climatic gradients) can be ruled out. From a management/conservation perspective, one might expect similar communities in each individual pond (judging by their similarity in morphological features and their same age) and therefore overall a limited added value emerging from a cluster of such habitats. However, for all groups, our study clearly shows a high species replacement among ponds. The landscape-level species inventory for all groups therefore seems to depend on the existence of multiple habitats. Currently, a major issue related to secondary habitats is whether they can be considered solely as supplementary habitats for the natural ones, or whether they function as a standalone network (Chester and Robson, 2013). Here we have shown that the bomb crater ponds are hosting a considerable share of the species set of natural habitats and can therefore be considered as their partial replacement. At the same time, they also func-

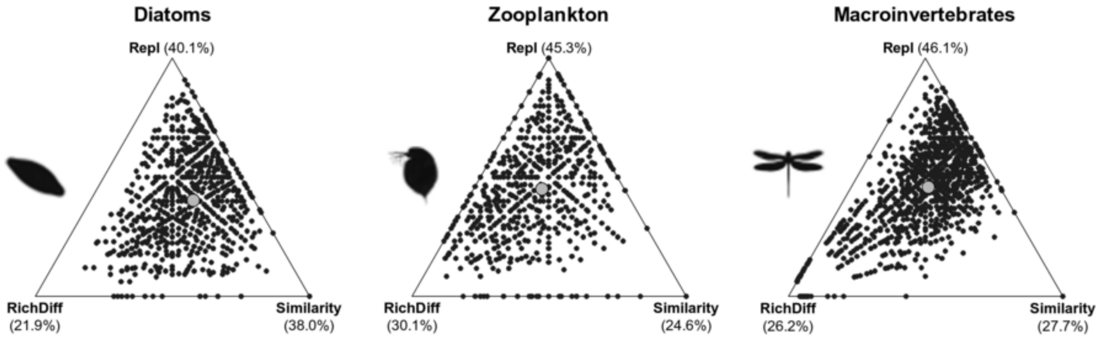

Fig. 4. SDR-simplices for benthic diatoms, zooplankton and macroinvertebrates. Each small dot (black) represents a pair of sites, while the large dots (grey) stand for the mean values of the additive components (RichDiff – richness difference, Repl – species replacement). The mean percentage value of each additive component is given in brackets.

tion as an independent habitat network that is capable of maintaining high gamma diversity.

Ponds are highly dynamic ecosystems with pronounced annual and inter-annual changes in environmental conditions (Hassall et al., 2012). Taxa living in (temporary) ponds are adapted to environmental fluctuations and compensate frequent local extinctions by fast re-colonization (Frisch and Green, 2007; Jeffries, 1994). Rescue effects through dispersal among ponds may be favoured in a dense pond network as in our study, where there are several habitat patches, and their availability (due to drying out or changing local conditions) for specific taxa might change with time. The short distances between ponds ease (re-)colonization for both actively and passively dispersing taxa in the network (patch dynamics).

5. Conclusions and implications for conservation

We showed that the explicit consideration of beta diversity along with its components might provide important insights for assessment and management of protected areas. In spite of sampling data from a cluster of morphologically similar habitats situated in close proximity, we found a high degree of spatial compositional turnover. The overall outstanding importance of species replacement in all organism groups strongly underlies the importance of conserving all ponds as a network, as the high gamma diversity seen here can only be sustained by a high number of sites. This finding is an important message for habitat management, given that recent pond conservation actions are generally site-specific, i.e. trying to prioritize ponds according to their local species richness and composition, while ignoring spatial community turnover (Hill et al., 2016). We found different degree of congruence among the three investigated groups regarding their diversity patterns along environmental gradients. This supports the importance of simultaneously considering multiple organism groups, each of which with their specific traits that can provide a more comprehensive understanding on the most important environmental factors that should be maintained for high gamma diversity across taxa.

Besides the high overall gamma diversity across the investigated organism groups, the bomb crater ponds proved to be important surrogate habitats, hosting even regionally and globally rare species. Based on these, we argue that they do not deserve their negative reputation. The bomb crater ponds studied here act today as unusual and distinctive reservoirs for temporary water biodiversity, being a partial replacement for the lost natural habitats. Considering the serious losses of ponds in Europe, they should be deemed as habitats of outstanding value, treated as core areas of pond conservation, particularly when occurring in dense clusters as in our study area.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.02.025.

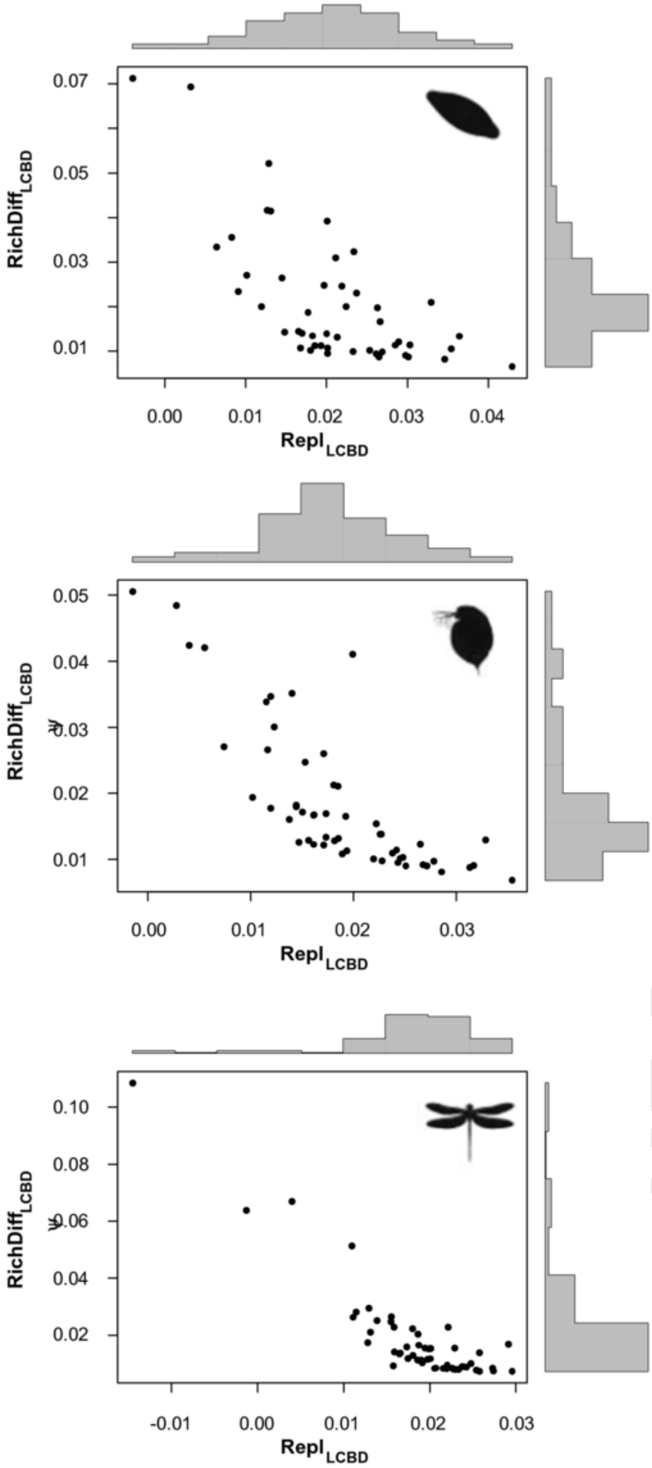

Fig. 5. The local contribution of richness difference ($\text{RichDiff}_{\text{LCBD}}$) vs species replacement ($\text{Repl}_{\text{LCBD}}$) to total beta diversity together with the distribution frequency of the values of these two indices among the ponds. Separate plots show the results for diatoms, zooplankton and macroinvertebrates.

Table 3
Significant predictors of local species richness (alpha diversity), local contribution to beta diversity (LCBD) and the two components (replacement, richness difference) of LCBD in each of the investigated organism group, resulting from generalized additive models (F and p values refer to explanatory variables, while adjusted R^2 is the whole model). For models with no significant variable, we show the model parameters with the last (non-significant) variable that was retained in the sequential backward selection. Abbreviations: TP – total phosphorus, cond – conductivity, DIN – dissolved inorganic nitrogen, Z – water depth, area - total surface area. Direction of the relationships is indicated with "-" for negative and "+" for positive and "∪" for U-shaped relationship (added in brackets).

	Variable	F	p	R^2 adj.
Species richness (alpha diversity)				
Benthic diatoms	TP (−)	11.38	***	0.33
Zooplankton	cond (−)	8.36	**	0.48
	DIN (−)	7.59	**	
	TP (−)	5.38	*	
Macroinvertebrates	cond (−)	7.70	**	0.42
	DIN (−)	8.50	**	
	Z (+)	4.60	*	
Local contribution to beta diversity (LCBD)				
Benthic diatoms	cond (∪)	18.60	***	0.43
	TP (+)	7.14	**	
Zooplankton	cond (∪)	11.65	***	0.38
	Z (−)	6.26	*	
Macroinvertebrates	cond (∪)	7.50	**	0.36
	Z (−)	10.10	**	
Replacement component of LCBD				
Benthic diatoms	cond (∪)	6.81	**	0.20
Zooplankton	DIN (−)	1.62	ns	0.01
Macroinvertebrates	area (−)	7.58	**	0.11
Richness difference component of LCBD				
Benthic diatoms	TP (+)	4.94	*	0.08
Zooplankton	cond (∪)	7.50	**	0.20
Macroinvertebrates	Z (−)	2.68	ns	0.03

Significance levels: 'ns' $p > 0.1$, '.' $p < 0.1$, '*' $p < 0.05$, '**' $p < 0.01$, '***' $p < 0.001$.

References

Airoldi, L., Balata, D., Beck, M.W., 2008. The Gray Zone: relationships between habitat loss and marine diversity and their applications in conservation. J. Exp. Mar. Biol. Ecol. 366, 8–15. http://dx.doi.org/10.1016/j.jembe.2008.07.034 (Marine ecology: A tribute to the life and work of John S. Gray).

Al-Shami, S.A., Heino, J., Che Salmah, M.R., Abu Hassan, A., Suhaila, A.H., Madrus, M.R., 2013. Drivers of beta diversity of macroinvertebrate communities in tropical forest streams. Freshw. Biol. 58, 1126–1137. http://dx.doi.org/10.1111/fwb.12113.

Becerra-Jurado, G., Harrington, R., Kelly-Quinn, M., 2012. A review of the potential of surface flow constructed wetlands to enhance macroinvertebrate diversity in agricultural landscapes with particular reference to Integrated Constructed Wetlands (ICWs). Hydrobiologia 692, 121–130. http://dx.doi.org/10.1007/s10750-011-0866-2.

Beja, P., Alcazar, R., 2003. Conservation of Mediterranean temporary ponds under agricultural intensification: an evaluation using amphibians. Biol. Conserv. 114, 317–326. http://dx.doi.org/10.1016/S0006-3207(03)00051-X.

Belk, D., 1998. In: Witham, C.W., Bauder (Eds.), Global Status and Trends in Ephemeral Pool Invertebrate Conservation: Implications for Californian Fairy Shrimp. pp. 147–150.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Weatherby, A., 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. Aquat. Conserv. Mar. Freshwat. Ecosyst. 15, 693–714.

Boros, E., Horváth, Z., 2013. Aquatic vertebrates: fishes (Pisces), amphibians (Amphibia) and reptiles (Reptilia). In: Boros, E., Ecsedi, Z., Oláh, J. (Eds.), Ecology and Management of Soda Pans in the Carpathian Basin. Hortobágy Environmental Association, Balmazújváros, pp. 112–113.

Boros, E., Nagy, T., Pigniczki, C., Kotymán, L., V-Balogh, K., Vörös, L., 2008. The effect of aquatic birds on the nutrient load and water quality of soda pans in Hungary. Acta Zool. Acad. Sci. Hung. 54, 207–224.

Boros, E., Horváth, Z., Wolfram, G., Vörös, L., 2014. Salinity and ionic composition of the shallow astatic soda pans in the Carpathian Basin. Ann. Limnol. Int. J. Limnol. 50, 59–69. http://dx.doi.org/10.1051/limn/2013068.

Boven, L., Stoks, R., Forró, L., Brendonck, L., 2008. Seasonal dynamics in water quality and vegetation cover in temporary pools with variable hydroperiods in Kiskunság (Hungary). Wetlands 28, 401–410. http://dx.doi.org/10.1672/06-174.1.

Boven, L., Vanschoenwinkel, B., De Roeck, E.R., Hulsmans, A., Brendonck, L., 2008. Diversity and distribution of large branchiopods in Kiskunság (Hungary) in relation to local habitat and spatial factors: implications for their conservation. Mar. Freshw. Res. 59, 940–950. http://dx.doi.org/10.1071/MF08154.

Brooks, R.T., 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. Clim. Chang. 95, 469–483. http://dx.doi.org/10.1007/s10584-008-9531-9.

Céréghino, R., Ruggiero, A., Marty, P., Angélibert, S., 2008. Biodiversity and distribution patterns of freshwater invertebrates in farm ponds of a south-western French agricultural landscape. Hydrobiologia 597, 43–51. http://dx.doi.org/10.1007/s10750-007-9219-6.

Céréghino, R., Boix, D., Cauchie, H.-M., Martens, K., Oertli, B., 2014. The ecological role of ponds in a changing world. Hydrobiologia 723, 1–6. http://dx.doi.org/10.1007/s10750-013-1719-y.

Chester, E.T., Robson, B.J., 2013. Anthropogenic refuges for freshwater biodiversity: their ecological characteristics and management. Biol. Conserv. 166, 64–75. http://dx.doi.org/10.1016/j.biocon.2013.06.016.

Cozma, N.J., Juhász, P., Müller, Z., Olajos, P., Kiss, B., 2014. The true bug (Heteroptera: Nepomorpha, Gerromorpha) fauna of some soda pans and sodic water bodies of Great Hungarian Plain. Nat. Somogy. 25, 41–50.

Csabai, Z., Gidó, Z., Szél, G., 2002. Vízibogarak kishatározója II. (Coleoptera: Georissidae, Spercheidae, Hydrochidae, Helophoridae, Hydrophilidae) [A guide for the identification of water beetles of Hungary - in Hungarian with English abstract], Vízi természet- és környezetvédelem. Környezetgazdálkodási Intézet, Budapest.

Csarmann, E., 2008. Ökologie von Amphibien in ausgewählten Lacken des Seewinkels (dipl). University of Vienna, Vienna.

Davies, B., Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Sear, D., Bray, S., Maund, S., 2008. Comparative biodiversity of aquatic habitats in the European agricultural landscape. Agric. Ecosyst. Environ. 125, 1–8. http://dx.doi.org/10.1016/j.agee.2007.10.006.

De Bie, T., Declerck, S., Martens, K., De Meester, L., Brendonck, L., 2007. A comparative analysis of cladoceran communities from different water body types: patterns in community composition and diversity. Hydrobiologia 597, 19–27. http://dx.doi.org/10.1007/s10750-007-9222-y.

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., Declerck, S.A.J., 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol. Lett. 15, 740–747.

De Marco, P.J., 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., Oertli, B., 2013. Patterns in the organization of Cerrado pond biodiversity in Brazilian pasture landscapes. Hydrobiologia 723, 87–101. http://dx.doi.org/10.1007/s10750-013-1695-2.

De Meester, L., Declerck, S., Stoks, R., Louette, G., Van De Meutter, F., De Bie, T., Michels, E., Brendonck, L., 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. Aquat. Conserv. Mar. Freshwat. Ecosyst. 15, 715–725. http://dx.doi.org/10.1002/aqc.748.

Downing, J.A., 2010. Emerging global role of small lakes and ponds: little things mean a lot. Limnetica 29, 9–24.

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M., Middelburg, J.J., 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol. Oceanogr. 51, 2388–2397. http://dx.doi.org/10.4319/lo.2006.51.5.2388.

Downing, J.A., Cole, J.J., Middelburg, J.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Prairie, Y.T., Laube, K.A., 2008. Sediment organic carbon burial in agriculturally eutrophic impoundments over the last century. Glob. Biogeochem. Cycles 22, GB1018http://dx.doi.org/10.1029/2006GB002854.

Eaton, A.D., Clesceri, L.S., Rice, E.W., Greenberg, A.E. (Eds.), 2005. Standard Methods for the Examination of Water and Wastewater, 21st ed., APHA, AWWA, WEF, Washington, DC, USA.

Eder, E., Hödl, W., 2002. Large freshwater branchiopods in Austria: diversity, threats and conservational status. In: Escobar-Briones, E., Alvarez, F. (Eds.), Modern Approaches to the Study of Crustacea. Springer US, pp. 281–289.

Fairbanks, D.H.K., Reyers, B., van Jaarsveld, A.S., 2001. Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. Biol. Conserv. 98, 365–379. http://dx.doi.org/10.1016/S0006-3207(00)00179-8.

Fontaneto, D., De Smet, W.H., Ricci, C., 2006. Rotifers in saltwater environments, re-evaluation of an inconspicuous taxon. J. Mar. Biol. Assoc. U. K. 86, 623–656. http://dx.doi.org/10.1017/S0025315406013531.

Forró, L., 2000. Checklist, distribution maps and bibliography of large branchiopods in Hungary (Anostraca, Notostraca, Spinicaudata, Laevicaudata). Misc. Zool. Hung. 13, 47–58.

Frisch, D., Green, A.J., 2007. Copepods come in first: rapid colonization of new temporary ponds. Fundam. Appl. Limnol. 168, 289–297. http://dx.doi.org/10.1127/1863-9135/2007/0168-0289.

Gallego, I., Davidson, T.A., Jeppesen, E., Pérez-Martínez, C., Sánchez-Castillo, P., Juan, M., Fuentes-Rodríguez, F., León, D., Peñalver, P., Toja, J., Casas, J.J., 2012. Taxonomic or ecological approaches? Searching for phytoplankton surrogates in the determination of richness and assemblage composition in ponds. Ecol. Indic. 18, 575–585. http://dx.doi.org/10.1016/j.ecolind.2012.01.002.

Gascón, S., Machado, M., Sala, J., Cancela da Fonseca, L., Cristo, M., Boix, D., 2012. Spatial characteristics and species niche attributes modulate the response by aquatic passive dispersers to habitat degradation. Mar. Freshw. Res. 63, 232–245. http://dx.doi.org/10.1071/MF11160.

Gołdyn, B., Bernard, R., Czyż, M.J., Jankowiak, A., 2012. Diversity and conservation status of large branchiopods (Crustacea) in ponds of western Poland. Limnol. Ecol. Manag. Inland Waters 42, 264–270. http://dx.doi.org/10.1016/j.limno.2012.08.006 (The eyes of the landscape – the value of ponds in the 21st century).

Hammer, U.T., 1986. Saline Lake Ecosystems of the World. Springer.

Hassall, C., 2014. The ecology and biodiversity of urban ponds. Wiley Interdiscip. Rev. Water 1, 187–206. http://dx.doi.org/10.1002/wat2.1014.

Hassall, C., Hollinshead, J., Hull, A., 2012. Temporal dynamics of aquatic communities and implications for pond conservation. Biodivers. Conserv. 21, 829–852. http://dx.doi.org/10.1007/s10531-011-0223-9.

Heino, J., 2010. Are indicator groups and cross-taxon congruence useful for predicting biodiversity in aquatic ecosystems?. Ecol. Indic. 10, 112–117.

Heino, J., Grönroos, M., 2017. Exploring species and site contributions to beta diversity in stream insect assemblages. Oecologia 183, 151–160. http://dx.doi.org/10.1007/s00442-016-3754-7.

Hill, M.J., Ryves, D.B., White, J.C., Wood, P.J., 2016. Macroinvertebrate diversity in urban and rural ponds: Implications for freshwater biodiversity conservation. Biol. Conserv. 201, 50–59. http://dx.doi.org/10.1016/j.biocon.2016.06.027.

Hofmann, G., Werum, M., Lange-Bertalot, H. (Eds.), 2011. Diatomeen im Süßwasser-Benthos von Mitteleuropa. Bestimmungsflora Kieselalgen für die Ökologische Praxis. Über 700 der häufigsten Arten und Ihre Ökologie. A.R.G. Gantner Verlag K.G., Ruggell, Liechtenstein.

Horváth, Z., Vad, C.F., 2015. Life history and current distribution of the fairy shrimp Chirocephalus carnuntanus (Brauer, 1877) (Crustacea: Anostraca). N. West J. Zool. 11, 102–109.

Horváth, Z., Vad, C.F., Vörös, L., Boros, E., 2013. The keystone role of anostracans and copepods in European soda pans during the spring migration of waterbirds. Freshw. Biol. 58, 430–440. http://dx.doi.org/10.1111/fwb.12071.

Horváth, Z., Vad, C.F., Vörös, L., Boros, E., 2013. Distribution and conservation status of fairy shrimps (Crustacea: Anostraca) in the astatic soda pans of the Carpathian basin: the role of local and spatial factors. J. Limnol. 72, 103–116. http://dx.doi.org/10.4081/jlimnol.2013.e9.

Horváth, Z., Vad, C.F., Tóth, A., Zsuga, K., Boros, E., Vörös, L., 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. http://dx.doi.org/10.1111/j.1600-0706.2013.00575.x.

ISO, 1984. Determination of Ammonium. Part 1. Manual Spectrometric Method. ISO 7150-1:1984. International Standardization Organization, Geneva, 7.

IUCN, 2016. The IUCN Red List of Threatened Species. Version 2016.2 [WWW Document]. URL http://www.iucnredlist.org/search (accessed 11.24.16).

Jeffries, M., 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshw. Biol. 32, 603–612. http://dx.doi.org/10.1111/j.1365-2427.1994.tb01151.x.

Jeffries, M.J., Epele, L.B., Studinski, J.M., Vad, C.F., Batzer, D., 2016. Invertebrates in temporary wetland ponds of the temperate biomes. In: Boix, D. (Ed.), Invertebrates in Freshwater Wetlands. Springer International Publishing, pp. 105–139.

Knutson, M.G., Richardson, W.B., Reineke, D.M., Gray, B.R., Parmelee, J.R., Weick, S.E., 2004. Agricultural ponds support amphibian populations. Ecol. Appl. 14, 669–684. http://dx.doi.org/10.1890/02-5305.

Kovács-Láng, E., Molnár, E., Kröel-Dulay, G., Barabás, S. (Eds.), 2008. The KISKUN LTER: Long-term Ecological Research in the Kiskunság, Hungary. Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót.

Ladányi, Z., Blanka, V., Meyer, B., Mezősi, G., Rakonczai, J., 2015. Multi-indicator sensitivity analysis of climate change effects on landscapes in the Kiskunság National Park, Hungary. Ecol. Indic. 58, 8–20. http://dx.doi.org/10.1016/j.ecolind.2015.05.024.

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Glob. Ecol. Biogeogr. 23, 1324–1334. http://dx.doi.org/10.1111/geb.12207.

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. http://dx.doi.org/10.1111/ele.12141.

Lemmens, P., Mergeay, J., De Bie, T., Van Wichelen, J., De Meester, L., Declerck, S.A.J., 2013. How to maximally support local and regional biodiversity in applied conservation? Insights from pond management. PLoS One 8, e72538http://dx.doi.org/10.1371/journal.pone.0072538.

Levkov, Z., 2009. Amphora sensu lato. In: Diatoms of Europe: Diatoms of the European Inland Waters and Comparable Habitats. A.R.G. Gantner Verlag K.G., Ruggell, Liechtenstein.

Lukács, B.A., Sramkó, G., Molnár, V.A., 2013. Plant diversity and conservation value of continental temporary pools. Biol. Conserv. 158, 393–400. http://dx.doi.org/10.1016/j.biocon.2012.08.024.

Maloufi, S., Catherine, A., Mouillot, D., Louvard, C., Couté, A., Bernard, C., Troussellier, M., 2016. Environmental heterogeneity among lakes promotes hyper β-diversity across phytoplankton communities. Freshw. Biol. 61, 633–645. http://dx.doi.org/10.1111/fwb.12731.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253. http://dx.doi.org/10.1038/35012251.

McKnight, M.W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S., Stuart, S.N., 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. PLoS Biol. 5, e272http://dx.doi.org/10.1371/journal.pbio.0050272.

Mimouni, E.-A., Pinel-Alloul, B., Beisner, B.E., 2015. Assessing aquatic biodiversity of zooplankton communities in an urban landscape. Urban Ecosyst. 1–20. http://dx.doi.org/10.1007/s11252-015-0457-5.

MSZ EN, 2014. Water Quality. Guidance for the Routine Sampling and Preparation of Benthic Diatoms From Rivers and Lakes. MSZ EN 13946:2014. Hungarian Standards Institution, Budapest, 18.

Oertli, B., Biggs, J., Céréghino, R., Grillas, P., Joly, P., Lachavanne, J.-B., 2005. Conservation and monitoring of pond biodiversity: introduction. Aquat. Conserv. Mar. Freshwat. Ecosyst. 15, 535–540. http://dx.doi.org/10.1002/aqc.752.

Oertli, B., Céréghino, R., Hull, A., Miracle, R., 2009. Pond conservation: from science to practice. Hydrobiologia 634, 1–9. http://dx.doi.org/10.1007/978-90-481-9088-1_14.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. Vegan: Community Ecology Package. R Package Version 2.0-7.

Paavola, R., Muotka, T., Virtanen, R., Heino, J., Kreivi, P., 2003. Are biological classifications of headwater streams concordant across multiple taxonomic groups?. Freshw. Biol. 48, 1912–1923. http://dx.doi.org/10.1046/j.1365-2427.2003.01131.x.

Petri, A.P., Holló, I., Nagy-László, Z., Deák, C., 2012. Dél-alföldi szikes jelleggel összefüggésbe hozható állóvizek makroszkopikus gerinctelen faunájának összehasonlítása [Comparative analysis of the macroinvertebrate fauna of ponds related to salinisation in the South part of Great Hungarian Plain]. Acta Biol. Debrecina Suppl. Oecologica Hung. 28, 141–165.

Podani, J., Schmera, D., 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. Oikos 120, 1625–1638.

Qiao, X., Li, Q., Jiang, Q., Lu, J., Franklin, S., Tang, Z., Wang, Q., Zhang, J., Lu, Z., Bao, D., Guo, Y., Liu, H., Xu, Y., Jiang, M., 2015. Beta diversity determinants in Badagongshan, a subtropical forest in central China. Sci. Rep. 5, 17043. http://dx.doi.org/10.1038/srep17043.

Ruhí, A., San Sebastian, O., Feo, C., Franch, M., Gascon, S., Richter-Boix, A., Boix, D., Llorente, G., 2012. Man-made Mediterranean temporary ponds as a tool for amphibian conservation. Ann. Limnol. 48, 81–93. http://dx.doi.org/10.1051/limn/2011059.

Sartory, D.P., Grobbelaar, J.U., 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114, 177–187. http://dx.doi.org/10.1007/BF00031869.

Scheiner, D., 1974. A modified version of the sodium salicylate method for analysis of wastewater nitrates. Water Res. 8, 835–840. http://dx.doi.org/10.1016/0043-1354(74)90030-X.

Schouten, M.A., Barendregt, A., Verweij, P.A., Kalkman, V.J., Kleukers, R.M.J.C., Lenders, H.J.R., Siebel, H.N., 2010. Defining hotspots of characteristic species for multiple taxonomic groups in the Netherlands. Biodivers. Conserv. 19, 2517–2536. http://dx.doi.org/10.1007/s10531-010-9857-2.

Shulse, C.D., Semlitsch, R.D., Trauth, K.M., Williams, A.D., 2010. Influences of design and landscape placement parameters on amphibian abundance in constructed wetlands. Wetlands 30, 915–928. http://dx.doi.org/10.1007/s13157-010-0069-z.

da Silva, P.G., Hernández, M.I.M., 2015. Scale-dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches. PLoS One 10, e0123030http://dx.doi.org/10.1371/journal.pone.0123030.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should Beta-diversity inform biodiversity conservation?. Trends Ecol. Evol. 31, 67–80. http://dx.doi.org/10.1016/j.tree.2015.11.005.

Stenger-Kovács, C., Lengyel, E., 2015. Taxonomical and distribution guide of diatoms in soda pans of Central Europe. Stud. Bot. Hung. 46, 3–203. http://dx.doi.org/10.17110/StudBot.2015.46.Suppl.3.

Tóth, A., Horváth, Z., Vad, C.F., Zsuga, K., Nagy, S.A., Boros, E., 2014. Zooplankton of the European soda pans: fauna and conservation of a unique habitat type. Int. Rev. Hydrobiol. 99, 255–276. http://dx.doi.org/10.1002/iroh.201301646.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, D., 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biol. Conserv. 115, 329–341. http://dx.doi.org/10.1016/S0006-3207(03)00153-8.

Williams, P., Biggs, J., Nicolet, P., 2010. New clean-water ponds—a way to protect freshwater biodiversity. Br. Wildl. 22, 77–85.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B Stat Methodol. 73, 3–36. http://dx.doi.org/10.1111/j.1467-9868.2010.00749.x.

Wood, P.J., Greenwood, M.T., Barker, S.A., Gunn, J., 2001. The effects of amenity management for angling on the conservation value of aquatic invertebrate communities in old industrial ponds. Biol. Conserv. 102, 17–29. http://dx.doi.org/10.1016/S0006-3207(01)00087-8.

Wood, P.J., Greenwood, M.T., Agnew, M.D., 2003. Pond biodiversity and habitat loss in the UK. Area 35, 206–216. http://dx.doi.org/10.1111/1475-4762.00249.

Zacharias, I., Zamparas, M., 2010. Mediterranean temporary ponds. A disappearing ecosystem. Biodivers. Conserv. 19, 3827–3834. http://dx.doi.org/10.1007/s10531-010-9933-7.