

## Artificial ponds in Central Europe do not fall behind the natural ponds in terms of macrophyte diversity

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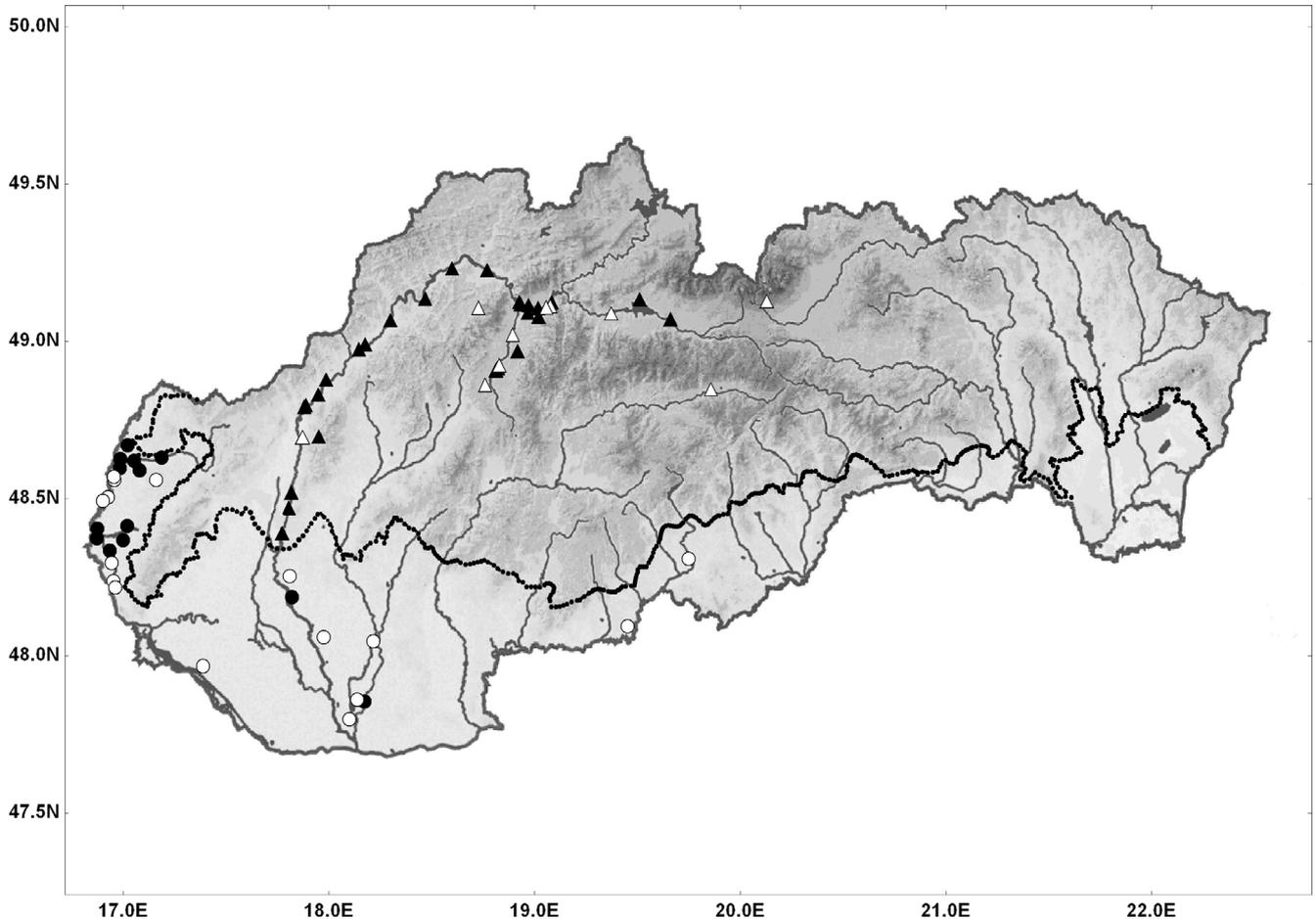
**Abstract** – We studied macrophyte composition and 24 environmental variables in 69 ponds of both natural and artificial origin in Slovakia. We tested differences in  $\alpha$  and  $\gamma$  diversity and  $\beta$  similarity between natural and artificial ponds for helophytes, hydrophytes, red list species and all species. We also assessed effects of environmental variables on species richness of studied ponds by generalised linear models (GLM). For local diversity, the significant difference was obtained only in case of helophytes. Beta similarity significantly differed for all the species groups. Total species numbers (gamma diversity) of all the groups were higher in natural ponds with the exception of hydrophytes. A randomization test of  $\gamma$  diversity yielded significant differences for helophytes and all species groups; richness and diversity of hydrophytes and red list species were not significantly different. Thus, we can conclude that even though natural ponds have a significantly higher regional diversity, local diversity is comparable not only for common species but also endangered red-listed macrophytes and thus artificial ponds could serve as proper secondary habitats for macrophytes. GLM showed different effect of environmental predictors on richness of studied species and pond groups and a slightly higher explained variability in natural (40%) compared to artificial (37%) ponds.

**Keywords:** comparative diversity / lentic habitats / aquatic plants / species richness

**Résumé** – Les mares artificielles d'Europe centrale ne sont pas en retard par rapport aux mares naturelles en termes de diversité des macrophytes. Nous avons étudié la composition des macrophytes et 24 variables environnementales dans 69 mares d'origine naturelle et artificielle en Slovaquie. Nous avons testé les différences de diversité  $\alpha$  et  $\gamma$  et de similitude  $\beta$  entre les mares naturelles et artificielles pour les hélrophytes, les hydrophytes, les espèces de la liste rouge et toutes les espèces. Nous avons également évalué les effets des variables environnementales sur la richesse en espèces des mares étudiées à l'aide de modèles linéaires généralisés (GLM). En ce qui concerne la diversité locale, une différence significative n'a été obtenue que dans le cas des hélrophytes. La similarité bêta était significativement différente pour tous les groupes d'espèces. Le nombre total d'espèces (diversité gamma) de tous les groupes était plus élevé dans les mares naturelles, à l'exception des hydrophytes. Un test de randomisation de la diversité  $\gamma$  a produit des différences significatives pour les hélrophytes et tous les groupes d'espèces; la richesse et la diversité des hydrophytes et des espèces de la liste rouge n'étaient pas significativement différentes. Par conséquent, nous pouvons conclure que même si les mares naturelles présentent une diversité régionale nettement plus grande, la diversité locale est comparable non seulement pour les espèces communes, mais aussi pour les macrophytes inscrits sur la liste rouge, ce qui fait que les mares artificielles pourraient servir d'habitats secondaires appropriés pour les macrophytes. Les modèles linéaires généralisés ont montré différents effets des variables environnementales prédictives de la richesse des espèces et des groupements de mares étudiées et une variabilité naturelle (40%) légèrement plus élevée que celle des mares artificielles (37%).

**Mots-clés :** diversité comparative / habitats lenticques / plantes aquatiques / richesse spécifique

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**Fig. 1.** Location of studied localities in Slovakia. Circles and triangles represent localities in Pannonian and Carpathian region, respectively; empty symbols indicate waterbodies with natural origin, solid artificial ponds. Dotted line represent border between bioregions.

## 1 Introduction

Intensive limnological research during recent decades has brought several studies which state that ponds play an irreplaceable role in maintaining macrophyte diversity in landscape (Oertli *et al.*, 2002; Biggs *et al.*, 2005; 2017; Céréghino *et al.*, 2014). Together with the facts that ponds have a greater total area than lakes on a global scale (Downing *et al.*, 2006), and a smaller catchment area in comparison with other aquatic ecosystems such as rivers (Davies *et al.*, 2008b), small standing inland waters encourage for their protection. Smaller catchments are less exposed to the harmful effects of human activities such as use of fertilisers or waste discharge, and more isolated smaller waterbodies enhance aquatic diversity heterogeneity and species composition (Akasaka and Takamura, 2012; Waldon, 2012). Such information is very useful in the case of nature protection. Generally, freshwaters belong to the most threatened ecosystems worldwide due to climate change, direct destruction by man or natural succession changes (Millennium Ecosystem Assessment, 2005; Dudgeon *et al.*, 2006). Along with freshwaters decline aquatic macrophytes are also vanishing. In addition to natural ponds, scientific attention has recently focused also on artificial ponds as potentially biodiversity valuable habitats

(Chester and Robson, 2013). Due to diverse range of environmental conditions in artificial waterbodies, it is probably impossible to unambiguously confirm the importance of such ponds for maintaining aquatic macrophyte diversity without taking into account the waterbody specifics. Some kinds of human influences and local management, such as bankside angling, biomass removal or extensive fish farming are beneficial for macrophytes (Linton and Goulder, 2000; Broyer and Curtet, 2012; Šumberová *et al.*, 2012) because they limit successional changes (Dodds and Whiles, 2010; Sayer *et al.*, 2012). On the other hand, some harmful consequences are linked to management practices such as dense fish stocks and manipulation of water regimes, or indirect influences resulting from intensive agriculture leading to the eutrophication of water (Crivelli, 1983; Scheffer and Carpenter, 2003; Declerck *et al.*, 2006; Akasaka *et al.*, 2010; Kadoya *et al.*, 2011). Moreover, stabilisation of banks in waterbodies causes a loss of littoral ecotones with a negative impact on macrophyte occurrence in ponds (Kadoya *et al.*, 2008, 2011; Zelnik *et al.*, 2012).

Despite the fact that several studies have pointed out that artificial ponds are suitable refuges for macrophytes (Gee *et al.*, 1997; Spałek, 2006; Chester and Robson, 2013), critical assessments of their real contribution to species diversity at local, among-site or regional levels have so far been

**Table 1.** Summary characteristics of environmental variables. Mean values with range (in the brackets) are displayed. Asterisks in the column “M–W test” indicate significant result of Mann–Whitney  $U$  test for comparison of variables ( $^*p < 0.05$ ,  $^{**}p < 0.01$ ,  $^{***}p < 0.001$ ,  $ns$  = non-significant difference,  $x$  = categorical variable). Mann–Whitney  $U$  test was not applied for categorical variables banks, bioregion and connectivity variables.

Variable characteristics	Artificial (n = 43)	Natural (n = 26)	M-W test
Altitude (m a.s.l.)	200 (110-594)	163 (108-1219)	ns
Gradual or Steep bank	.	.	×
Carpathian or Pannonian	.	.	×
Type of connectivity (1 = main channel to 3 separated pond)	3 (2-3)	3 (2-3)	×
Cover of man-made structures in 100 metres from the sampling site (%)	5 (0-95)	0 (0-45)	**
Cover of fields in 100 metres from the sampling site (%)	0 (0-95)	0 (0-70)	ns
Cover of forests in 100 metres from the sampling site (%)	30 (0-100)	35 (4-100)	ns
Cover of meadows in 100 metres from the sampling site (%)	10 (0-90)	20 (0-95)	ns
Cover of wetlands in 100 metres from the sampling site (%)	0 (0-99.5)	15 (0-70)	ns
Content of water ammonia	0.07 (0-3.11)	0.31(0-4.34)	*
Content of water nitrite	0.05 (0-0.43)	0.03 (0-0.42)	ns
Content of water nitrate	0.65 (0.02-8.3)	0.62 (0-5.43)	ns
Content of water phosphates	0.08 (0-1.08)	0.13 (0-2.75)	ns
Shading by woody vegetation (higher than 3 metres) on banks (%)	60 (0-100)	92.5 (0-100)	**
Cover of coarse substrate on the bottom (%; cf. Janauer 2003)	0 (0-60)	0 (0-10)	ns
Cover of fine substrate on the bottom (%; cf. Janauer 2003)	10 (0-100)	100 (10-100)	***
Cover of gravel on the bottom (%; cf. Janauer 2003)	2 (0-100)	0 (0)	***
Cover of sand on the bottom (%; cf. Janauer 2003)	0 (0-30)	0 (0)	**
Water conductivity ( $\mu\text{S}\cdot\text{cm}^{-1}$ )	464.3 (63.5-1445)	516.1 (20.3-1986.5)	ns
Average water depth (cm)	140 (22-300)	64.4 (19-145.8)	***
Water reaction	8.1 (6.91-9.44)	7.525 (5.61-8.9)	**
Type of water regime (1= permanently waterlogged to 4 = dried every year)	1 (1-2)	2 (1-3)	×
Water temperature ( $^{\circ}\text{C}$ )	20.1 (13.9-28.8)	19.6 (14-26.4)	ns
Turbidity of water (1= clear to 4 = turbid)	2 (1-4)	2 (1-4)	ns

unsatisfactory. None of these studies directly compared diversity between natural and artificial ponds, with authors stating that artificial ponds are suitable refuges for both common and endangered macrophytes and that they are species rich. Moreover, there is a large number of studies exploring how environmental factors shape species composition or diversity both in natural (Toivonen and Huttunen, 1995; Della *et al.*, 2008; Lukács *et al.*, 2015) and artificial ponds (Edwardsen and Økland, 2006; Broyer and Curtet, 2012; Wezel *et al.*, 2014), but comparisons of factors among ponds with different origins are relatively few.

The aims of our study were to: (i) characterise environmental conditions and diversity of macrophytes in the studied artificial and natural ponds and test whether there are any differences between artificial and natural lentic waterbodies, and (ii) to identify how environmental factors shape species diversity in ponds with different origins.

## 2 Methods

### 2.1 Study area and data sampling

The study was carried out in two Central European bioregions – the Pannonian and the Western Carpathian (hereafter as the Carpathian; European Commission, 2014) – which provide heterogeneous landscape mosaics as well as a

wide range of ecological gradients. We selected small ponds (standing waters with area in the range 0.05–2 ha, *cf.* Biggs *et al.*, 2005) of both artificial and natural origin in Slovakia (Fig. 1). Artificial ponds as man-made aquatic habitats were represented by flooded gravel pits, mud pits and fishponds. Natural ponds within our study comprised oxbows ponds and flooded terrain depressions. Altogether, 69 ponds were inspected, 43 were artificial and 26 were ponds of natural origin. In each pond, all macrophyte species (including bryophytes, vascular plants and macroscopic algae from Charales order) were recorded. Macrophyte survey was performed by wading or from a boat using a rake within one randomly selected isosceles triangle-shaped sampling area of 100 m<sup>2</sup> with the base following the pond margin and apex in the middle of the pond (Williams *et al.*, 2004). Physicochemical, hydrological and landscape variables (Tab. 1) were collected in each pond. Water conductivity, pH and temperature were measured directly in the field by the portable CyberScan PC 650 device. Altitude was recorded by a Garmin GPS device. Water samples (100 ml) were taken from three randomly selected locations at each sampling site. Samples were homogenized and frozen for further laboratory analysis of ammonium nitrogen ( $\text{NH}_4^+$ ), nitrate nitrogen ( $\text{NO}_3^-$ ), nitrite nitrogen ( $\text{NO}_2^-$ ) and orthophosphate content ( $\text{PO}_4^{3-}$ ) (*cf.* Hrivnák *et al.*, 2013). To reduce seasonality, all these measurements as well as water sampling were performed

**Table 2.** Summary table of species diversity and results of tests of potential differences between artificial and natural ponds. Local diversity is presented by mean numbers of species at one locality and by results of permutational ANOVA used for testing of differences between artificial and natural ponds. Beta similarity is presented by mean Jaccard's index, differences were tested with test of multivariate homogeneity of variances ten times with randomly selected subsets due to uneven samples, *p*-values are represented. Gamma diversity shows total species numbers per species groups with *p*-values obtained in randomization test. Asterisks indicate statistically significant results, for details about tests see data analysis part in methods section.

Diversity/similarity	Species group	Artificial (n = 43)	Natural (n = 26)	Tests results		
				p-value	R Sum Sq	Mean Sq
Local (alpha) diversity	All species	3.2	5	0.98	0.00	0.0042
	Helophytes	0.7	1.8	0.04*	17.025	17.0247
	Hydrophytes	2.5	3.2	0.14	8.38	8.3796
	Red list species	0.7	1	0.25	1.336	1.33573
				p-value		
Among-site (beta) similarity	All species	0.125	0.069	0.023–0.001*		
	Helophytes	0.046	0.022	0.001*		
	Hydrophytes	0.150	0.097	0.848–0.001*		
	Red list species	0.042	0.027	0.005–0.001*		
				p-value		
Regional (gamma) diversity	All species	39	51	0.005*		
	Helophytes	12	24	0.001*		
	Hydrophytes	27	27	.		
	Red list species	11	13	0.105		

during vegetation sampling in the summer, repeated in the end of the summer (during September and early October) and mean values of two measurements were used for analysis. Average water depth was calculated from the measurements at 10 randomly selected locations within the sampling site. Percentage cover of five categories of land use (LU), (1) forests and bushes, (2) wetlands, (3) pastures, meadows and orchards, (4) agricultural fields and (5) built-up area was estimated within 100 m from the ponds. Shading of woody vegetation was estimated as percent cover of shrubs and trees on the banks higher than 3 m. Percentage cover of fine, sand, gravel and coarse bottom substrate was estimated (Janauer, 2003). Type of water regime was estimated on the scale from 1 to 4 (1 = permanently waterlogged, 4 = dried every year) based on our repeated visits of the studied ponds during several years. Bank slope was visually estimated as gradual or steep with threshold 20°.

Nomenclature of plant species is in accordance with the checklist of Marhold and Hindák (1998), and the category of threat with the actual Slovak Red lists (Hindák and Hindáková, 2001; Eliáš *et al.*, 2015).

## 2.2 Data analysis

To exclude highly correlated ( $r > 0.8$ ) variables, we assessed relationships between pairs of variables by non-parametric Spearman's correlation coefficient. None of the variables was highly correlated with another, so all the variables (with exception of cover of sand and gravel substrate in natural ponds because those variables had zero values) were used for further analysis.

Environmental variables were tested for differences between artificial and natural ponds by a nonparametric

Mann–Whitney *U* test due to prevailing non-normality in the dataset.

Then, variables were transformed for improving homoscedasticity where necessary. Log transformation was used for cover of fine and sand substrate, and altitude; for all types of LU and content of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$  and  $\text{PO}_4^{3-}$ , cube root transformation was used.

The species occurrence data were split into four presence/absence matrices. The first matrix was composed of helophyte species, the second of hydrophytes (true aquatic species), the third of both species categories and the fourth represented red list species. Classification of helophyte and hydrophyte species groups was based on previous studies (Alahuhta *et al.*, 2012; Landucci *et al.*, 2015; Kolada, 2016); 15 recorded non-wetland or non-aquatic species were excluded from the dataset (Appendix A). Next, we conducted analyses for comparison of diversity between artificial and natural ponds. Local (alpha,  $\alpha$ ) diversity was defined as raw species number within the sampling area in individual ponds. For testing possible differences in alpha diversity between artificial and natural ponds, we ran a one-way ANOVA with origin of pond as a fixed effect. Firstly, we conducted the Bartlett test for checking the homogeneity of variances. Due to non-normality of the dataset, a permutational ANOVA was applied. Among-site (beta,  $\beta$ ) similarity was described by Jaccard's index, and a test of multivariate homogeneity of variances by the function betadisper (Oksanen *et al.*, 2016) was run for testing possible differences between pond types. Because of uneven samples of pond types we randomly selected 26 localities from subset of artificial ponds and repeated testing ten times (every time with new randomly selected subset). Regional (gamma,  $\gamma$ ) diversity was the total richness of all sites within one pond type. We ran a randomization test based on differences between total

**Table 3.** Final selected significant variables for GLM explaining local diversity in ponds with explained percent deviation ( $D\%$ ). Signs “+” and “-” indicate positive or negative effect on  $\alpha$ -diversity. Variable characteristics and values are in Table 1.

Pond type	Species group	Variables	D%
Artificial ponds	All species	LU – Field (+)	21.3
	Helophytes	LU – Field (+), NO <sub>2</sub> content (-)	37.2
	Hydrophytes	Water turbidity (-)	12.5
	Red list species	Altitude (+)	12.7
Natural ponds	All species	Shading (-), substrate – fine (+), connectivity (-)	40.6
	Helophytes	Shading (-), substrate – fine (+), bank – gradual (+)	43.1
	Hydrophytes	Shading (-)	15
	Red list species	Water turbidity (-)	14.4

richness of pond types for testing possible differences between pond types using the *c2cv* function (Rossi, 2011).

Species richness (defined as raw count of species within a sampling area in an individual pond) was modelled separately for each species group and type of pond (altogether 8 models) using generalised linear models (GLM) with an assumed Poisson distribution and log link function (McCullagh and Nelder, 1989) and with backward stepwise selection. Firstly, the  $p$ -value was set to  $<0.15$  for including potentially meaningful variables, and then for final models we assessed the  $p$ -value at  $<0.05$ .

All analyses were performed in R software (R Core Team, 2016), using the libraries *vegan* (Oksanen *et al.*, 2016), *lmPerm* (Wheeler and Torchiano, 2016) and *Rich* (Rossi, 2011). Results were considered as significant at  $\alpha = 95\%$ .

### 3 Results

#### 3.1 Environmental characteristics of ponds

The artificial and natural ponds significantly differed in 8 environmental variables. Artificial ponds occurred in man-modified areas and that fact was reflected by higher share of the agricultural field and artificial type of landscape in the vicinity of ponds and lower shading by bank vegetation. Sand and gravel substrates did not occur in any of the natural ponds and in contrast, the cover of fine substrate was higher in natural ponds. Water pH and content of  $\text{NH}_4^+$  differed between pond types with higher concentrations of  $\text{NH}_4^+$  in natural and higher pH in artificial ponds. Water was significantly deeper in artificial ponds which were mainly permanent, while natural ponds were shallower and with more fluctuating water level (Tab. 1).

#### 3.2 Species richness and diversity of ponds

Altogether, 60 species were found (Tab. A.1). The most frequent species were *Myriophyllum spicatum* (29% of ponds), *Ceratophyllum demersum* (20%), *Lemna minor* (17%) and *Phragmites australis* (12%); 19 species occurred at single site only. The average number of species per pond was 3.9 with a range from 0 to 20 species. From a total number of 16 red-list species, 13 were found in natural and 11 in artificial ponds.

Mean  $\alpha$ -diversity in case of all species group was higher in natural ponds than in artificial ponds. Natural ponds were

richer than artificial ponds in number of all species, helophytes and red-list species (Tab. 2).

Permutational ANOVA yielded significant differences only for the helophytes, while hydrophytes, red-list species and overall species number were not significantly different between artificial and natural ponds (Tab. 2).

The highest mean  $\beta$ -similarity (0.15) was observed in hydrophytes in artificial ponds, while red list species in natural ponds showed the lowest (0.03)  $\beta$ -similarity. A test of multidimensional dispersion showed significant differences for all species, helophytes and red-list species groups;  $\beta$ -similarity of hydrophytes also differed but from 10 randomly selected subsets only six showed significant difference and four not (Tab. 2).

Regional diversity was higher for all species, helophytes and red-list species in natural ponds, while  $\gamma$ -diversity of hydrophytes was the same for both pond types. Randomization tests showed significant differences in all species and helophytes,  $\gamma$ -diversity of hydrophytes was the same for both pond types and for red-list species was not significantly different between artificial and natural ponds (Tab. 2).

#### 3.3 Effect of environmental variables on species richness

Final models obtained from GLM (Tab. 3) totally differed in significant predictors of  $\alpha$ -diversity between pond types. In artificial ponds, only the model for the helophytes consisted of two significant variables (nitrite content with negative and LU fields with positive influence) and explained the most deviation (37.2%); for other species groups, only one predictor was significant and the percentage of explained deviation was lower. For natural ponds, models for all species and helophytes contained three significant predictors and both models explained about 40% of the deviation; for hydrophytes and red-list species, only one variable was significant (shading and water turbidity for hydrophytes and red-list species, respectively) and models showed about 15% of explained deviation.

## 4 Discussion

### 4.1 Species diversity

Comparing species richness of ponds in Europe, we can state that ponds in Slovakia are species poorer than adequate waterbodies from neighbouring countries such as Poland or

Hungary (Bosiacka and Pieńkowski, 2012; Szoszkiewicz *et al.*, 2014; Lukács *et al.*, 2015) and the rest of Europe (Oertli *et al.*, 2002; Gledhill *et al.*, 2008; Chappuis *et al.*, 2012). Generally, the eastern part of Europe is known for lower macrophyte species richness (Chappuis *et al.*, 2012) and higher species richness in Hungary or Poland could be influenced by inclusion of all observed species, not only true aquatic plants or helophytes. However, a potential weakness of such comparison is in fact that cited surveys were focused mainly on ponds and lakes with area more than two hectares; macrophyte richness increases with area (Jones *et al.*, 2003) so effect of pond area on species richness should be taken account. Also presence of alien aquatic species and species with Atlantic or Boreal distribution can play important role. Number of aquatic alien species in Slovakia is much lower than in Hungary (Medvecká *et al.*, 2012; Lukács *et al.*, 2016). Atlantic and boreal aquatic plant species, which are relatively frequent in Poland, are absent in Western Carpathian region in Slovakia (*cf.* Otaheľová in Valachovič, 1995; Matuszkiewicz, 2008).

We studied whether artificial ponds differ from natural ponds in the case of all three types of biodiversity (local, among-site, regional) and thus whether they are an appropriate substitution for maintaining macrophyte diversity in consideration of the declining quantity and quality of natural ponds.

Macrophyte local ( $\alpha$ ) diversity was higher in natural ponds for all species groups, but a significant difference was obtained for the helophytes only. Thus, artificial ponds are equal in comparison with natural ponds in the case of  $\alpha$ -diversity. Based on our results, significantly lower counts of helophytes were caused by the common absence of gradual banks and shallow littoral zone in artificial waterbodies mainly in case of gravel or mud pits. Moreover, relatively shallow water and fluctuating water regime in natural ponds enhances the colonisation by helophytes in littoral zone (Nicolet *et al.*, 2004; Rhazi *et al.*, 2012; Lukács *et al.*, 2013). In addition to mentioned characteristics, higher variance of water reaction and higher ammonia content in case of natural ponds can play important role for presence of broader groups of macrophytes including helophytes (*cf.* Lacoul and Freedman, 2006; Kolada, 2016). From conservation point of view, finding that local diversity of endangered species did not significantly differ between artificial and natural ponds is positive. Lower counts of helophytes in artificial ponds had no effect in the case of endangered species because only *Butomus umbellatus* belong to both helophytes and red list species groups. Although a prevailing kind of consensus resulting from previous surveys assesses artificial lentic waterbodies as comparable to the natural ones (Wezel *et al.*, 2014), no direct comparison supported by statistical tests exists. Studies were focused on comparative diversity of ponds with other aquatic ecosystems like streams, rivers or ditches with a conclusion of high  $\alpha$ -diversity and counts of endangered species in ponds; however, authors included both natural and artificial standing waters into the dataset (Williams *et al.*, 2004; Biggs *et al.*, 2005; Biggs *et al.*, 2007; Davies *et al.*, 2008a, Davies *et al.*, 2008b). Other authors (*e.g.* Hrivnák *et al.*, 2014) found that waterbodies with artificial origin had higher species richness than those with natural origin. However, artificial waterbodies included mainly habitats with standing or slow running water (ponds, canals), while natural origin combined habitats with running (streams, rivers) and standing (river

oxbows) water. Moreover, streams and rivers belong to relatively species poor aquatic ecosystems in Central Europe (Svitok *et al.*, 2016).

Macrophyte among-site ( $\beta$ ) similarity showed slightly higher Jaccard's index in artificial ponds with significantly different values for all studied species groups. Previously discussed heavy modifications narrow amount of species with ability to grow in artificial ponds which resulted in more unified macrophyte communities there. Thus, we can assume that even though artificial ponds seems to be more diverse in habitat conditions resulting from their varied origins, local environment is relatively unified across broader area. In spite of this statement, artificial ponds can be important secondary aquatic habitats for the survival of macrophytes. Due to good spreading ability of aquatic plant species (Figuerola *et al.*, 2005; Neff and Baldwin, 2005), artificial ponds could serve as reservoirs of diaspores for potential further colonisation of distant aquatic habitats.

Natural ponds also showed higher regional ( $\gamma$ ) diversity which significantly differed from artificial ponds in all species and helophytes. Higher total species numbers were found despite the relatively lower number of localities for natural ponds. This fact indirectly supports the previously stated importance of ponds for maintaining aquatic biodiversity (Oertli *et al.*, 2002; Biggs *et al.*, 2005; Cérèghino *et al.*, 2014) because a relatively low number of localities of natural ponds harboured comparable species counts found during previous surveys in Slovakia with more sampling sites (Otaheľová *et al.*, 2007; Svitok *et al.*, 2016). Similarly to  $\alpha$ -diversity, artificial ponds held markedly lower helophytes  $\gamma$ -diversity which influenced and caused a significant difference in species pool of all species. Surprisingly, the number of hydrophytes was the same for both pond types (27 species) and numbers of red-list species (13 and 11 for natural and artificial ponds, respectively) were not significantly different. This leads to the conclusion that the main difference between artificial and natural ponds is the occurrence of helophytes which are limited in artificial waterbodies mainly by unsuitable bank morphology, greater depth and less frequent season water fluctuation comparing to natural ponds.

## 4.2 Alpha diversity and environmental variables

The positive effect of fields and no negative influence by urbanised areas in the vicinity of ponds on  $\alpha$  diversity was the interesting result obtained in GLM. Heavily modified surrounding landscape is undoubtedly considered as a factor causing diversity loss in waterbodies, due to increasing eutrophication as a consequence of fertiliser and sewage runoff (Carpenter *et al.*, 1998; Scheffer and Carpenter, 2003; Akasaka *et al.*, 2010). Moreover, the negative effect of nitrite content on helophyte diversity was observed. Thus, we assume that the positive effect of fields on macrophyte diversity in artificial ponds is mainly in suppression of shading or providing organic litter (Barko and Smart, 1983; Lacoul and Freedman, 2006). Whilst shading was a negative factor affecting diversity of all species, helophytes and hydrophytes in natural ponds. Another remarkable finding is the positive effect of altitude on diversity of red-list species in artificial ponds because diversity decrease as a consequence of higher elevation is well known

(Hinden *et al.*, 2005; Lacoul and Freedman, 2006). Altitude range was probably insufficient to show those negatives and presumably the hidden effect of strong human utilisation in lower altitudes across factors such as presence of fields in lowlands and related nutrient runoff that leads to a positive effect of altitude on diversity in artificial ponds. As discussed above, the importance of substrate in lentic waterbodies is mainly in providing nutrients rather than for assisting rooting. The occurrence of fine substrate increases species diversity in both lotic and lentic waterbodies (Svitok *et al.*, 2016). Here, we found a positive influence on diversity of all species and in combination with gradual banks also for helophytes in natural ponds. Generally, non-modified banks in natural habitats offer suitable conditions such as shallow water or fine substrate for proper development of helophyte communities (Zelnik *et al.*, 2012). From the set of water characteristics, only turbidity had a significant negative impact on diversity of helophytes and red-list species in artificial and natural ponds, respectively. Turbidity is associated with light limitations which negatively affects macrophyte growth (Akasaka *et al.*, 2010, Kolada, 2016) including germination and growing of juvenile helophytes. Another factor related to turbidity is higher nutrient content (Lacoul and Freedman, 2006), which probably contributed to the negative effect of turbidity on red-list species. Proximity or connection with other waterbodies positively affects species composition *via* dispersal of individuals between habitats (Lacoul and Freedman, 2006; Akasaka and Takamura, 2012; Bosiacka and Pieńkowski, 2012; Waldon, 2012) which was also confirmed by positive effect of connectivity on diversity of all species in natural ponds where the higher level of isolation is the more negative effect on diversity.

## 5 Conclusions

Our study critically compared species diversity of aquatic macrophytes between artificial and natural ponds on environmental background in two bioregions of Central Europe. The main conclusion to be drawn from presented results is that artificial ponds are rather comparable to natural ones in the case of macrophyte species richness and diversity, and may serve as suitable secondary habitats for maintenance of aquatic plants. Such information is important due to the rapid decline of natural waterbodies in the cultural landscape during recent decades. Undoubtedly, artificial ponds could never absolutely substitute the natural ones due to limitations in development of new microhabitat or ecotones based on artificial origin; actually, this has reflected in a lower number of helophytes and resulting differences in all types of diversity for this species group. On the other hand, hydrophytes and red-list species showed the same or similar richness and with exception of  $\beta$ -similarity those groups did not differ between both pond types, which accurately highlights the role of anthropogenic waterbodies for maintaining macrophyte diversity. Furthermore, similarity was achieved despite the fact that pH values and depth, which are commonly important drivers of species composition in freshwater ecosystems (Lacoul and Freedman, 2006), significantly differed between pond types. Overall, from the set of 24 environmental factors according to GLM, only eight of them influenced  $\alpha$ -diversity in species groups.

This leads to the conclusion that even though artificial and natural ponds vary in environmental conditions and discrepant factors influence differently species groups, differences in diversity at all three levels (local, among-site and regional) are caused mainly by occurrence of different counts of helophyte species. Thus, we can confirm the importance of artificial standing waters for maintaining aquatic plant diversity at least in part of the Carpathian and Pannonian bioregions.

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## Appendices

### Appendix A List of observed species; asterisk indicates red-list species

**Table A.1.** The list of observed species.

Helophytes	Hydrophytes	Excluded species
* <i>Butomus umbellatus</i> L.	* <i>Batrachium aquatile</i> (L.) Dumort	<i>Agrostis stolonifera</i> L.
<i>Acorus calamus</i> L.	<i>Batrachium circinatum</i> (Sibth.) Spach	<i>Amblystegium riparium</i> (Hedw.) B. S. G.
<i>Alisma lanceolatum</i> With.	<i>Batrachium</i> sp.	<i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. Presl et C. Presl
<i>Alisma plantago-aquatica</i> L.	<i>Batrachium trichophyllum</i> (Chaix) Bosch	<i>Bidens frondosa</i> L.
<i>Bolboschoenus</i> sp. juv.	* <i>Callitriche cophocarpa</i> Sendtn.	<i>Brachythecium velutinum</i> (Hedw.) B. S. G.
<i>Carex acuta</i> L.	* <i>Callitriche palustris</i> L.	<i>Galium palustre</i> L.
<i>Carex elata</i> All.	<i>Ceratophyllum demersum</i> L.	<i>Hygrohypnum luridum</i> (Hedw.) Jenn.
<i>Carex pseudocyperus</i> L.	* <i>Ceratophyllum submersum</i> L.	<i>Lysimachia nummularia</i> L.
<i>Carex riparia</i> Curtis	<i>Elodea canadensis</i> Michx.	<i>Lythrum salicaria</i> L.
<i>Carex rostrata</i> Stokes ex With.	<i>Elodea nuttallii</i> (Planch.) H. St. John	<i>Myosotis palustris</i> Hill.
<i>Eleocharis acicularis</i> (L.) Roem. et Schult.	* <i>Hottonia palustris</i> L.	<i>Salix</i> sp. juv
<i>Eleocharis palustris</i> (L.) Roem. et Schult.	<i>Hydrocharis morsus-ranae</i> L.	<i>Sium latifolium</i> L.
<i>Equisetum fluviatile</i> L.	* <i>Chara foetida</i> A. Braun	<i>Solanum dulcamara</i> L.
<i>Glyceria declinata</i> Bréb.	* <i>Chara fragilis</i> Desv.	<i>Stellaria palustris</i> Retz.
<i>Glyceria maxima</i> (Hartm.) Holmb.	<i>Lemna minor</i> L.	<i>Warnstorfia exannulata</i> (B. S. G.) Loeske
<i>Iris pseudacorus</i> L.	<i>Lemna trisulca</i> L.	
<i>Juncus articulatus</i> L.	<i>Myriophyllum spicatum</i> L.	
<i>Pericaria amphibia</i> (L.) Delarbre	* <i>Myriophyllum verticillatum</i> L.	
<i>Pericaria hydropiper</i> (L.) Delarbre	* <i>Najas marina</i> L.	
<i>Phalaroides arundinacea</i> (L.) Rauschert	* <i>Nuphar lutea</i> (L.) Sm.	
<i>Phellandrium aquaticum</i> L.	* <i>Nymphaea alba</i> L.	
<i>Phragmites australis</i> (Cav.) Trin.	<i>Nymphaea</i> cult.	
<i>Rorippa amphibia</i> (L.) Besser	* <i>Potamogeton berchtoldii</i> Fieber	
<i>Sparganium emersum</i> Rehmman	<i>Potamogeton crispus</i> L.	
<i>Sparganium erectum</i> L.	<i>Potamogeton natans</i> L.	
<i>Typha angustifolia</i> L.	* <i>Potamogeton nodosus</i> Poir.	
<i>Typha latifolia</i> L.	<i>Potamogeton pectinatus</i> L.	
	<i>Potamogeton pusillus</i> L.	
	<i>Riccia fluitans</i> L. emend. Lorb.	
	<i>Spirodela polyrhiza</i> (L.) Schleid.	
	* <i>Trapa natans</i> L.	
	* <i>Utricularia australis</i> R. Br.	
	<i>Zannichelia pallustris</i> L.	

\* Red-list species.