



Macrophyte diversity of lakes in the Pannon Ecoregion (Hungary)



Balázs A. Lukács^{a,*}, Béla Tóthmérész^b, Gábor Borics^a, Gábor Várbíró^a, Péter Juhász^c,
Béla Kiss^c, Zoltán Müller^c, László G-Tóth^{d,e}, Tibor Erős^d

^a Department of Tisza River Research, MTA Centre for Ecological Research, 18/C Bem tér, Debrecen 4026, Hungary

^b MTA-DE Biodiversity and Ecosystem Services Research Group, Egyetem tér 1, Debrecen 4032, Hungary

^c Bio Aqua Pro Consulting Ltd., Soó Rezső u. 21, Debrecen 4032, Hungary

^d Balaton Limnological Institute, MTA Centre for Ecological Research, Klebelsberg K. u. 3, Tihany 8237, Hungary

^e Szent István University, Institute of Regional Economics and Rural Development, Gödöllő 2100, Hungary

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ABSTRACT

We examined the distribution of submerged and emergent macrophyte species and the entire macrophyte community within and between five lake types (highland reservoirs, alkali lakes, large shallow lakes, small to medium sized shallow lakes, marshes) in the Pannon Ecoregion, Hungary. The lowest submerged, emergent and total species richness was found in alkali lakes. The highest submerged macrophyte richness was in small to medium sized lakes, while the highest emergent macrophyte species richness was in reservoirs, small to medium sized lakes, and marshes. The values of within-lake type beta diversity were generally lower than the values of alpha diversity, especially for submerged macrophytes, indicating between site homogeneity in species composition within the lake types. Emergent macrophyte communities contributed the most to within and between lake type diversity and total (gamma) diversity. Canonical correspondence analyses showed that the main environmental variables which influenced the distribution of submerged macrophytes were conductivity, Secchi transparency and water nitrogen contents. For emergent macrophytes conductivity, lake width, altitude and water depth proved to be the most influential variables. Our results contribute to the knowledge of large-scale distribution of macrophytes in the Pannon Ecoregion and to the identification of conservation value of lakes using macrophytes. The results support the importance of small lakes and artificial lakes in the conservation of macrophyte diversity compared to large and natural lakes in the Pannon Ecoregion.

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1. Introduction

Freshwater biodiversity is declining at an alarming rate. This rate is much greater than has been noted for even in the most affected terrestrial systems (Millennium Ecosystem Assessment, 2005). To set conservation priorities for these valued ecosystems, it is essential to understand spatial variation in the diversity of organism groups in an array of freshwater habitat types (Underwood et al., 2000; Anderson et al., 2005). Standing waters have a major contribution to the biodiversity conservation of freshwater ecosystems, and with their variety in forms and habitat characteristics they provide diverse habitats for freshwater organisms. Evaluation of the contribution of various types of ponds and lakes to regional biodiversity has only recently been started to come to the forefront of research for conservation purposes (Biggs et al., 2005; De Meester et al., 2005; Williams et al., 2004).

It has long been recognized that standing waters play an important role in the conservation of aquatic plants (Linton and Goulder, 2000; Oertli et al., 2002; Nicolet, 2001; Nicolet et al., 2004). Several studies examined the regional scale diversity of macrophytes, focusing mainly on the question how diversity is related to environmental variables. It has been suggested that macrophyte distribution and diversity is mainly related to water transparency, conductivity, lake area, altitude and human pressures (Vestergaard and Sand-Jensen, 2000; Akasaka et al., 2010; Hicks and Frost, 2011). It is much less known how the diversity of macrophyte species is distributed in the landscape among the standing water habitat types, and how these patterns in diversity are related to the various life-forms of species. For example, the foremost life-forms of macrophytes are submerged and emergent, which have a fundamental role in creating the main zones in shallow lakes (upper-littoral and lower-littoral). However, the distribution of their species diversity is virtually unknown within and between habitat types.

The vanishing of macrophyte-rich habitats, such as marshes and small ponds, due to desiccation and drainage is a serious

* Corresponding author.

E-mail address: lukacs.balazs@okologia.mta.hu (B.A. Lukács).

Table 1
Overview of standing water types.

Code	Standing water type	Naturalness	Altitude (m)	Conductivity ($\mu\text{S cm}^{-1}$)	Water depth (m)	Secchi (m)	O ₂ content (mg l^{-1})	Lake zone	Number of lakes/sites
RES	Highland reservoirs	Artificial	237–554	166–1072	1.5–3	0.16–1.05	9.1–13.7	Pelagial	5/1
ALK	Alkali lakes	Natural	91–119	1849–6560	0.2–1	0.02–0.62	4.33–12.19	Littoral	11/1
BIG	Subbasins of Lake Balaton	Natural	98–118	774–1103	1.5–1.9	0.34–0.76	6.06–11.13	Pelagial	1/8
MED	Lowland small to medium size shallow lakes	Natural	83–213	200–1475	1.8–2.3	0.27–1.5	4.03–14.95	Pelagial	20/1
MARSH	Very shallow lakes	Natural	79–115	187–1184	0.05–1.2	0.05–1.2	0.25–6.4	Littoral	8/1

In the cells of the table minimum–maximum values are shown.

conservation problem. On the other hand, reservoirs built on streams for a variety of purposes (irrigation, flood control, fishing) may provide new artificial habitats for macrophytes (Céréghino et al., 2014), but the similarities and differences in their macrophyte diversity compared to that of the natural habitats should be directly quantified. Knowing the scale dependent relative contribution of alpha (mean local diversity) and beta (variation in species composition between sites or habitats) diversity to gamma diversity (total diversity within and between habitats) helps to define the relative value of different standing water habitat types in conserving macrophyte diversity and consequently, have the potential to help in optimizing conservation efforts at the regional scale. These issues can be effectively addressed using the method of diversity partitioning, which allows the quantification of the contributions of alpha and beta diversity to total diversity over a range of user-defined spatial scales. Thus, conservation biologists can set up priorities between sites and/or habitats across multiple scales (Gering et al., 2003).

The Pannon Ecoregion contains some unique standing water habitat types, which are rare (or missing) in other European regions. For example, many standing waters in the ecoregion have a peculiar astatic character (temporarily dried out) which is attributed to the arid continental climate (Szesztay, 1974; Horváth et al., 2013; Radulović et al., 2011). The climatic, geomorphologic and hydrologic features of standing waters resulted in a variety of lake types with well-developed submerged and emergent macrophyte vegetation. The purpose of this study is to quantify the contribution of artificial and natural lake types to the biodiversity of macrophytes in the Pannon Ecoregion, Hungary. Specifically, we (i) examined the distribution of submerged and emergent species in five habitat types (reservoirs, RES; alkali lakes, ALK; large shallow lakes, BIG; small to medium sized shallow lakes, MED; marshes, MARSH) to compare similarities and differences in their species diversity and composition and to select the most valuable types for conservation planning, and (ii) studied the relationship between the distribution of species and the basic physico-chemical characteristics of the studied standing waters.

2. Methods

2.1. Study area

The Pannon Ecoregion is located in the Carpathian Basin, Central Europe (EEA, 2009). Ninety per cent of the Ecoregion area is in Hungary and 10% in other countries (Austria, Czech Republic, Serbia, Slovakia, Ukraine and Romania). Two-thirds of the ecoregion is in the lowlands (200 m), the remaining area belongs to mid-altitude regions (200–800 m). Only a small proportion of the area belongs to submontane region (>500 m). Formerly almost the entire lowland area formed the floodplain of large alluvial rivers coming into the Carpathian Basin. Large-scale river regulations

altered the hydrological conditions of the landscape during the 19th century. These human perturbations led to the alteration or disappearance of natural habitats and to the development of new aquatic systems. As a consequence of the regulation of large potamal rivers certain types of standing waters were formed along the rivers (oxbow-lakes), while other types became scarce (alkali lakes) or disappeared (marshes).

Five habitat types were set up for Hungarian standing waters to obtain a useful landscape-level classification scheme based on the criteria outlined by Heino and Mykrä (2006), and using the top-down (system B) typology of the Water Framework Directive (Borics et al., 2014): reservoirs (RES); alkali lakes (ALK); lowland large shallow lakes (BIG), lowland small to medium sized shallow lakes (MED) and very shallow lakes (MARSH). Although the types have some overlapping physical characteristics, they can be easily distinguished based on some basic criteria (e.g. the status of naturalness, depth, see Table 1).

2.2. Site selection

Macrophyte data were collected during an ecoregion-wide survey of the biotic elements (ECOSURV Project 2005, <http://www.eu-wfd.info/ecosurv>). Aquatic macrophytes were studied in 52 standing water bodies all over Hungary (Fig. 1) in 2005 from the end of May to end of July, which is an appropriate time for field sampling. Sites were selected to represent the approximate ratio of the different lake types in the region. In case of large lakes (BIG), we used macrophyte data originated from the different basins (separated by an average distance of 12 km) of Lake Balaton, which is the largest shallow lake in Central Europe. We emphasize that the basins have differences in morphology, trophic state (Istvánovics et al., 2007) and are also separately handled in water management (VKKI, 2010a).

2.3. Macrophyte sampling

Macroalgae (*Chara* and *Cladophora* species) and vascular plants (submerged, floating, emergent and shoreline plants) were collected in transects. Prior to the establishment of transects the ratio of macrophyte coverage and the main types of macrophyte stands were checked using aerial photos. Five transects (100 m long and 3 m wide) were located from the open water to the outer edge of emergent vegetation, perpendicular to the shoreline following the protocol of Schaumburg et al. (2007). Emergent species spread beyond the shoreline to a maximum distance of 1–2 m (spray zone). In shallow lakes and marshes, the bottom-living plants were sampled by rakes, whereas in deeper waters a grapnel with a 10 m long rope was used. The field protocol with a five-level descriptor scale was used during field survey (Stelzer et al., 2005). Vascular plants were identified to species level using Király's (2009) handbook,

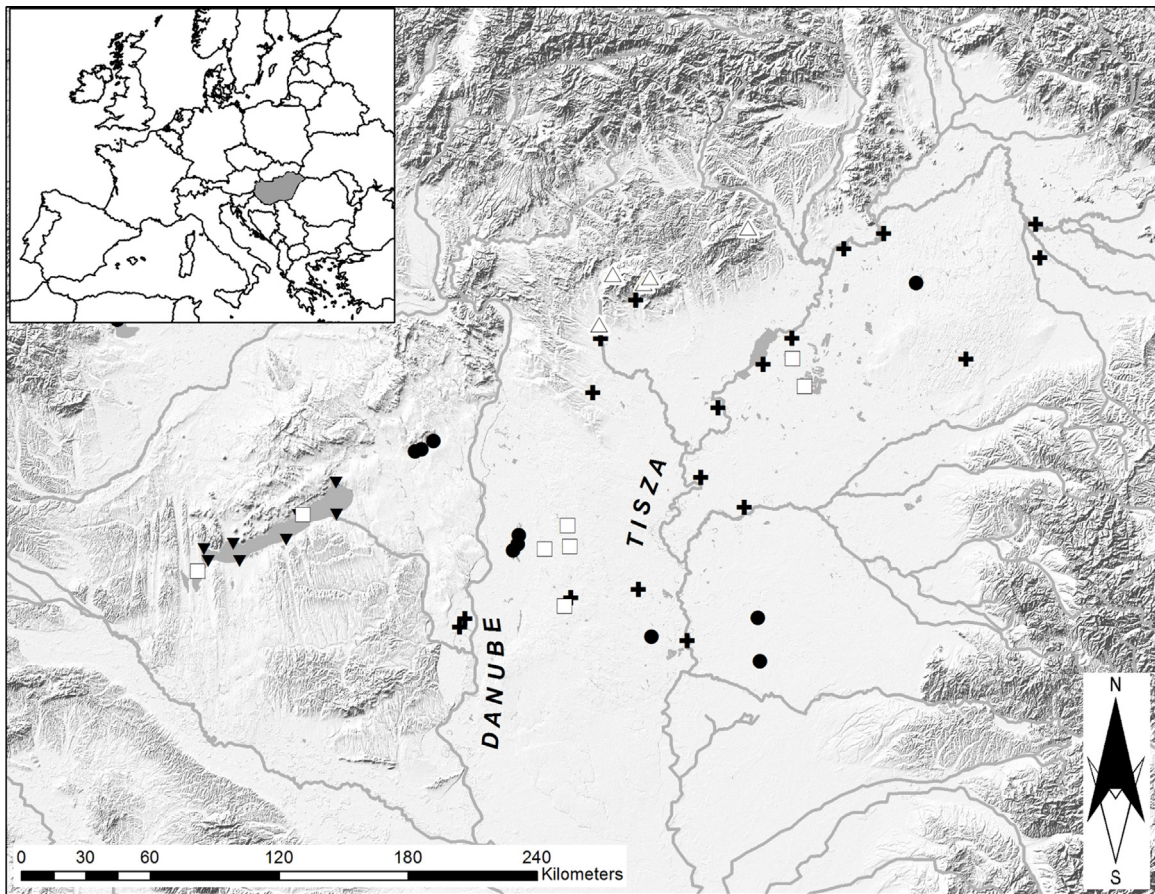


Fig. 1. Sampling sites in the Pannon Ecoregion. Notations: ● alkali lakes (ALK), □ Very shallow lakes (marshes) (MARSH), △ reservoirs (RES), ▼ lowland large shallow lakes (BIG), + lowland small shallow lakes (MED).

while Characeae and filamentous algae were identified to genus level.

We classified species into two functional groups, submerged and emergent, using life-form categories (Raunkjær, 1934) and moisture preference values (Ellenberg, 1974). *Ceratophyllids*, *elodeoids*, *isoetoids*, *lemnids*, *nymphaeids* and *charids* were considered as submerged. The moisture value in the submerged (i.e. hydrophytes) and in the emergent (i.e. helophytes) groups varied between 10–12 and 7–9, respectively.

2.4. Water samples and laboratory procedures

Water samples were collected by using a tube sampler at the time of the macrophyte survey from all lakes. Water temperature, conductivity, oxygen concentration, oxygen saturation and pH were measured on site, using a WTW Multi 340i multimeter. Secchi transparency, altitude and water depth were also recorded in the field. The surface area of lakes was determined after fieldwork using GIS. Concentrations of nitrite, nitrate, ammonium ions and the Kjeldahl-nitrogen, total-phosphorous and chlorophyll-a were determined in the laboratory by using manual spectrophotometric procedures. Table 2 contains the range of environmental variables of lake types.

2.5. Statistical analyses

Before any statistical analyses, we converted the ordinal-scale of the dataset into ratio-scale using the middle values of Braun-Blanquet's cover classes (Englone, 2012). We used the multiplicative way of diversity partitioning (Chao et al., 2012) to

determine the lakes' contribution to ecoregion level species diversity. We transformed the α - and β -diversity components into their number equivalents to let the α - and β -diversity component vary independently of each other (Jost, 2007). We defined β -diversity as the effective number of elements (i.e. effective number of distinct communities within and across the five lake types) (Tuomisto, 2010). We calculated β -diversity as: $\beta = \gamma/\alpha$, where γ is the total diversity of any lake types and α is the average diversity per sample unit.

Species abundance data were used for diversity calculations: (i) within a habitat type (alpha diversity); (ii) between lakes within a habitat type (beta1 diversity); (iii) between habitat types within the ecoregion (beta2 diversity) and (iv) for the whole ecoregion (total or gamma diversity). We considered three diversity indices, ranging from those that put more weight to species richness (number of species) to those that emphasize abundance ratios (frequent versus rare species) (Tóthmérész, 1995). Therefore, we used (i) the number of species; (ii) Shannon diversity (dominant and rare species are weighted equally) and (iii) Simpson diversity (weighted towards the frequent species) indices for diversity analyses.

All statistics were calculated for the submerged, emergent and entire species pool. Diversity calculations were made by Past 3 (Hammer et al., 2001). We used a variety of species richness estimation methods (Chao 1 (Chao, 1984), ACE, Jackknife 1, Jackknife 2, Bootstrap (for definitions see Colwell, 2005)) to compare observed and estimated species richness (i.e. total number of species) at both site (lake) and habitat type levels. Species richness estimation was made by EstimateS 7.5 (Colwell, 2005). To test the degree of similarity of the lake types and their separation ANOSIM (analysis of similarities) was performed (Clarke, 1993) on plant abundance

Table 2

Values of environmental variables of standing water types used in CCA.

Code	Area (ha)	NO ₂ (mg l ⁻¹)	NO ₃ (mg l ⁻¹)	NH ₄ (mg l ⁻¹)	Kjeldhal N (mg l ⁻¹)	Total-P (mg l ⁻¹)	Chlorophyll-a (mg l ⁻¹)
RES	1.81–183	0.014–0.024	1.23–3.31	0.01–0.06	0.73–2.3	0.085–0.53	5–10
ALK	39.86–7546.5	0.001–0.176	0.29–4.131	0.03–0.613	1.96–5.7	0.154–1.97	5–20
BIG	22,486–116,617	0.003–0.014	0.336–1.640	0.04–0.055	1.5–2.7	0.135–0.87	5–20
MED	4.28–3434	0.001–0.077	0.11–3.068	0.02–0.273	0.81–2.8	0.038–0.513	5–40
MARSH	25.17–5150	0.001–0.039	0.61–2.522	0.045–0.583	1.36–19.9	0.06–0.901	5–20

In the cells of the table minimum–maximum values are shown.

Table 3

The mean values of observed (Sobs) and estimated number of species for the submersed and entire species pool for the five habitat types using the estimators available in ESTIMATES software (for definitions see Colwell, 2005).

	N	Sobs	ACE	Chao 1	Jack 1	Jack 2	Bootstrap
<i>Hydrophyte</i>							
ALK	11	5.76	7.30	6.80	8.17	8.96	6.88
BIG	8	11.33	11.93	11.50	14.72	15.03	12.99
MED	20	21.57	22.48	22.23	27.12	28.14	24.35
MARSH	8	8.58	9.43	8.98	12.92	14.62	10.56
RES	5	3.68	4.12	3.68	5.82	6.68	4.63
<i>Total</i>							
ALK	11	29.84	39.66	35.49	45.56	54.26	36.66
BIG	8	42.36	48.15	46.48	54.80	56.54	48.39
MED	20	88.10	98.31	96.46	113.80	122.81	100.26
MARSH	8	56.31	65.28	64.53	78.16	84.79	66.44
RES	5	43.41	53.83	51.82	59.54	62.00	50.79

data. The null hypothesis of ANOSIM is that there are no differences between the members of the various groups. ANOSIM was calculated as: $[R = r_B - r_W / n(n-1)/4]$ where r_B and r_W are the means of the ranked Bray–Curtis similarities between groups and within groups, respectively, and n is the total number of samples. R scales from +1 to –1. An R value of +1 indicates that all the most similar samples are within the same groups. $R=0$ occurs if the high and low similarities are perfectly mixed and bear no relationship to the groups. A value of –1 indicates that the most similar samples are all outside of the groups. For simplicity, we show the results which were performed at the entire species pool level (i.e. did not distinguish submerged and emergent communities here). The ANOSIM analysis was also augmented by indicator species analysis (hereafter IndVal; Dufrêne and Legendre, 1997) to find significant indicator species for the habitat types. The best indicator species (i.e. symmetrical indicators) are those that occur only in a certain habitat type with high occurrence and abundance (see e.g. Dufrêne and Legendre, 1997; for more details).

We used canonical correspondence analysis (CCA) to assess the relationships between plant species and the measured environmental variables (ter Braak, 1986). Axes of the final ordination are restricted to the linear combinations of the environmental variables and the species data. In this way, the relationship between the two data sets can be directly compared. We determined significant variables by a forward selection of environmental variables in the CCA ordination (p -value = 0.05; 499 Monte Carlo permutations). All data used for the analysis were square root transformed. CCA and forward variable selection were made by CANOCO 4.5 (ter Braak and Šmilauer, 2002).

3. Results

3.1. Species pool

A total of 149 taxa were found in the 52 lakes of which 33 species were submerged and 116 species were emergent. The species richness of submerged macrophytes ranged from 0 to 13 (mean = 4.25 ± 0.51 SE; median = 3); species richness of emergent macrophytes ranged from 2 to 41 (mean = 17.36 ± 1.44 SE;

median = 15.5). The overall species richness of water bodies ranged from 2 to 53 (mean = 21.61 ± 1.78 ; median = 19.5). Differences between observed and estimated species richness values were low and showed consistent patterns among habitat types (Table 3), both according to the submerged and the entire species pool. Comparison of the observed species richness and the Chao 1 estimated values indicated that, on average, 87.5% of the entire species pool and 95.1% of the submerged macrophytes were collected in each habitat type.

3.2. Biodiversity partitioning

The lowest alpha diversity values for submerged, emergent and total species richness were found in ALK (Fig. 2a). The highest submerged species richness was found in MED, while the highest emergent species richness was found in RES, MED and MARSH habitats. The values of within-lake type beta diversity (beta1) were generally lower than the values of alpha diversity, indicating relatively low between site heterogeneity in species composition within the lake types. Mean within-site (alpha) diversity accounted the most for landscape-scale patterns (i.e. total among all lake types) in species richness for all community types (i.e. submerged, emergent and entire community) followed by between-site diversity (beta1) and then between lake type diversity (beta2).

The pattern in Shannon and Simpson diversity values (Fig. 2b and c, respectively) was similar between indices, but differed between submerged and emergent communities. The alpha and beta diversity of submerged species showed comparable values within habitat types. Emergent species showed relatively low alpha diversity values and very high beta diversity values within habitat types. Landscape-scale patterns in total Shannon and Simpson diversity mirrored within type patterns (Fig. 2). Specifically, for submerged species the relative contribution of alpha and beta1 diversity to total (gamma diversity) was largely the same, whereas for emergent species low alpha and very high beta1 values were observed. For the overall macrophyte community high alpha and low beta1 diversity values were found. Between types (beta2) diversity was low in all community types. These patterns in Shannon and Simpson diversity values highlight the differences in the

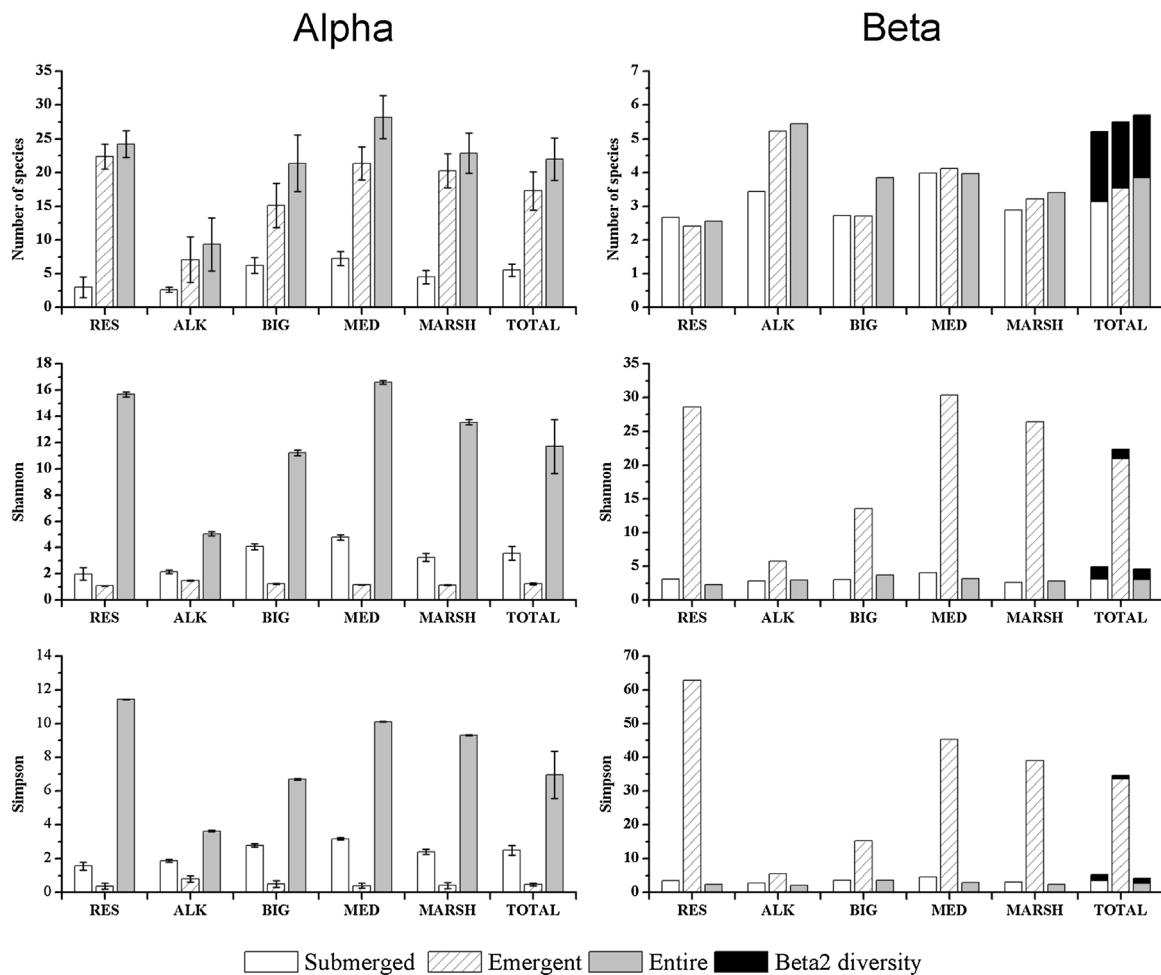


Fig. 2. Species richness, Shannon and Simpson diversity of standing water type's vegetation at submersed, emergent and entire species pool. Diversity indices were partitioned into within habitat type (alpha) diversity $\pm$ SE; between "lakes" within a habitat type (beta1) diversity and between habitat types within the ecoregion (beta2) diversity. RES, reservoirs; ALK, alkali lakes; BIG, subbasins of Lake Balaton; MED, lowland small to medium size shallow lakes; MARSH, very shallow lakes (marshes).

relative abundance distribution of species among both the community and the habitat types.

3.3. Macrophyte communities of lake types

The ANOSIM showed that all the lake types were significantly different based on their submersed macrophyte communities. Except BIG-MED, BIG-MARSH and MED-MARSH all lake types differed significantly by its emergent macrophyte communities (Table 4). The results of IndVal suggested *Bolboschoenus maritimus*, *Carex melanostachya*, *Potamogeton pectinatus* and *Schoenoplectus tabernaemontani* as characteristic species to ALKs. Indicator species of RESs were *Angelica sylvestris*, *Bidens tripartita*, *Carex vesicaria*, *Juncus inflexus*, *Juncus effusus*, *Myosotis palustris*, *Petasites hybridus*, *Poa palustris*, *Ranunculus repens*, *Scirpus sylvaticus* and *Scutellaria*

galericulata. Characteristic species of BIGs were *Myriophyllum spicatum*, *Potamogeton perfoliatus* and *Potamogeton pectinatus* ssp. *balatonicus*. Indicator species of MEDs were *Echinocystis lobata*, *Persicaria amphibia* and *Salvinia natans*. Characteristic species of MARSHs were *Galium palustre*, *Cirsium brachycephalum*, *Cirsium canum*, *Cladium mariscus* and *Valeriana officinalis* (see Electronic Appendix).

3.4. Species–environment relationships

The CCA analyses showed that the differences between lake types were lower based on submersed species, and higher based on the emergent species community (Fig. 3). The environmental variables that had strong correlation with Axes were summarized in Table 5. For submersed macrophytes the first two axes explained

Table 4

Similarities of sites (ANOSIM) for submersed ($R=0.3185$, $p=0.001$) and for the emergent species pool ($R=0.4090$, $p=0.001$).

	ALK	BIG	MED	MARSH
RES	0.568 [*] /0.899 [*]	0.751 [*] /0.653 [*]	0.609 [*] /0.512 [*]	0.414 [*] /0.705 [*]
ALK	–	0.650 [*] /0.404 [*]	0.573 [*] /0.540 [*]	0.609 [*] /0.502 [*]
BIG	–	–	0.311 [*] /0.126	0.675 [*] /0.098
MED	–	–	–	0.448 [*] /0.162

In the entries of the table the first figure is the similarity (R value) for the submersed and the second one is for the emergent species pool. Notations: RES, reservoirs; ALK, alkali lakes; BIG, lowland large shallow lakes; MED, lowland small to medium size shallow lakes; MARSH, very shallow lakes (marshes).

^{*} $p < 0.05$.

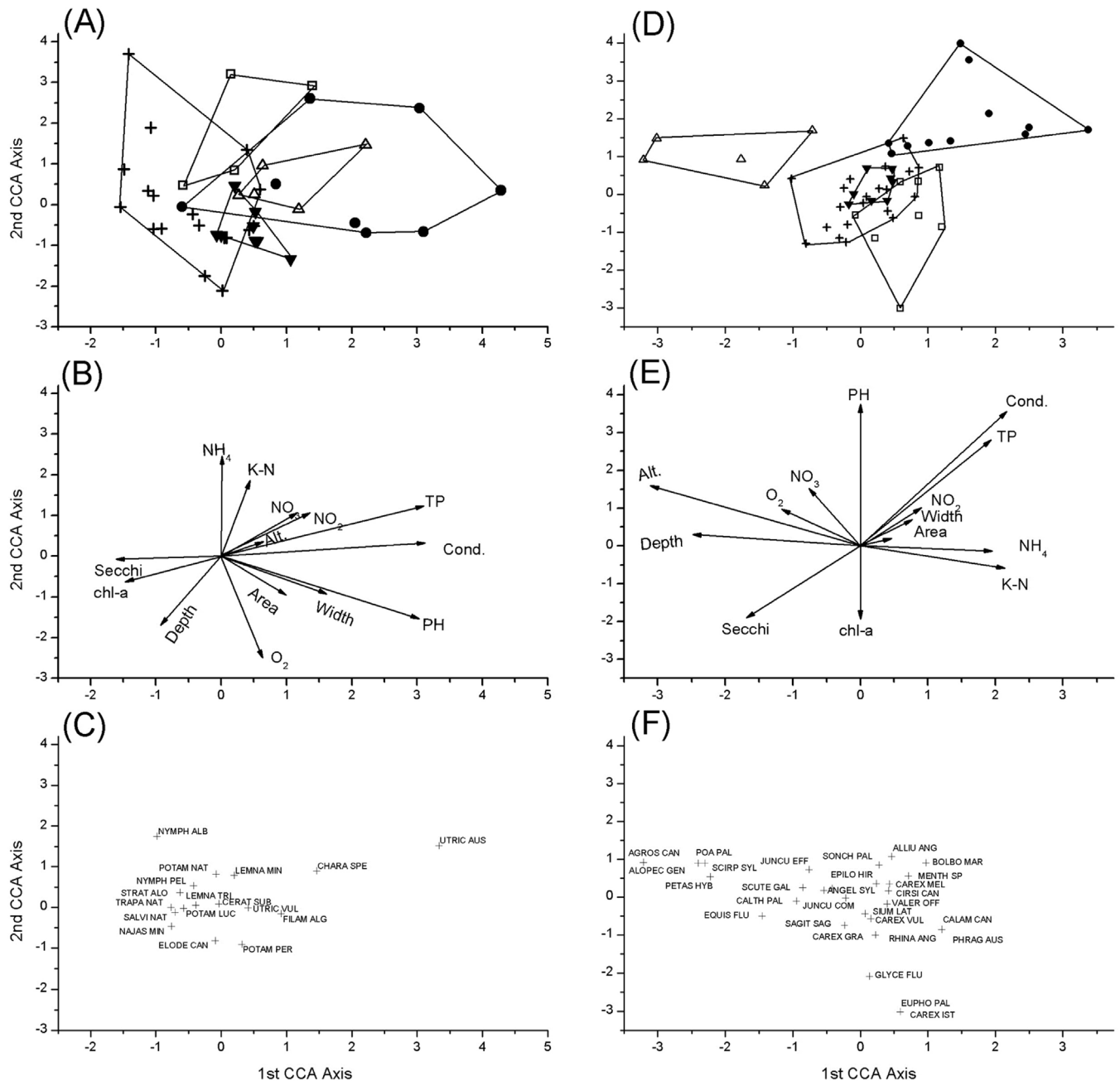


Fig. 3. Canonical correspondence analysis of plots, environmental data and species of the submerged (A, B, C) and emergent (D, E, F) species pool (explanatory values see in Table 5). Notations: Δ reservoirs (RES); $\bullet$ alkali lakes (ALK); $\blacktriangledown$ lowland large shallow lakes (BIG); $+$ lowland small to medium size shallow lakes (MED); $\square$ very shallow lakes (MARSH). TP, total phosphorous; Alt, altitude; chl-a, chlorophyll-a; Cond, conductivity; K-N, Kjeldahl nitrogen. Species names are formed by initial letters of the genus and species name.

18% and 14.3% of the total variance of species–environment relationships, respectively. Based on submerged macrophytes, sites were grouped into four highly overlapping groups, with a low differentiation of ALKs and MEDs along Axis 1, and a separation of MARSHs along Axis 2. BIGs were separated along Axis 3. RES was indistinct within these groups. ALKs were characterized by shallow depth, high conductivity values, low Secchi transparency, high concentration of nitrite and nitrate and low concentration of chlorophyll-a (Fig. 3). MEDs were characterized by higher depth and Secchi transparency, lower conductivity values and lower concentration of nitrite and nitrate.

For emergent macrophytes the first two axes explained 15.3% and 11% of variance. Based on emergent macrophytes, the 52 sites

were grouped into four overlapping point clouds (Fig. 3). ALKs and shallow lakes (BIG and MED) had a weak overlap but separated along Axis 1. MARSHs separated along Axis 2, while RESs separated along Axis 3. Shallow lakes (BIG and MED) characterized by high chlorophyll-a, Secchi transparency and large depth, but BIGs and MEDs were not separated according to their surface area. MARSHs were characterized by low pH and low concentration of nitrate. ALKs were characterized by high conductivity values. RESs were characterized by high altitude, high depth and high concentration of oxygen.

The forward selection of variables revealed different results for submerged and emergent species communities (Table 6). Significant predictors of the variability in the submerged species data

Table 5

Results of CCA for macrophyte communities for two dataset: submersed (33 species) and emergent (116 species).

	Submersed		Emergent	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue CCA	0.383	0.304	0.261	0.186
Species–environment correlation	0.910	0.875	0.910	0.912
Percent variance of species data	7.8	6.1	5.8	4.1
Percent variance of species–environment	18.0	14.3	15.3	10.9
Inter-set correlation of environmental variables with axes				
1. Altitude	0.18	0.08	−0.69	0.33
2. Water depth	−0.28	−0.34	−0.65	0.05
3. Lake width	0.29	−0.18	0.11	0.08
4. SECCHI	−0.39	0.06	−0.36	−0.33
5. Conductivity	0.68	0.03	0.40	0.54
6. pH	0.54	−0.31	0.008	0.57
7. Oxygen concentration	0.10	−0.47	−0.29	0.19
8. Lake area	0.16	−0.21	0.10	0.007
9. Nitrite	0.34	0.21	0.14	0.11
10. Nitrate	0.28	0.22	−0.12	0.26
11. Ammonia	0.07	0.47	0.30	−0.02
12. Kjeldhal-N	0.15	0.35	0.30	−0.09
13. Total-P	0.67	0.18	0.36	0.42
14. Chlorophyll-a	−0.40	−0.02	0.007	−0.37

Table 6

Ranking all environmental variables in importance in submersed and emergent macrophyte communities as obtained by forward selection on the CCA.

Variable	Lambda	p
<i>Hydrophytes</i>		
Total phosphorous	0.29	**
pH	0.2	**
Lake width	0.19	**
Ammonia	0.16	#
Oxygen conc.	0.15	n.s.
Altitude	0.13	n.s.
Water depth	0.15	n.s.
Chlorophyll-a	0.11	n.s.
Nitrate	0.11	n.s.
Conductivity	0.1	n.s.
Nitrite	0.1	n.s.
Lake area	0.09	n.s.
SECCHI depth	0.1	n.s.
Kjeldahl-N	0.07	n.s.
<i>Helophytes</i>		
Altitude	0.21	**
Lake depth	0.16	**
pH	0.14	**
Chlorophyll-a	0.13	*
Kjeldahl-N	0.13	#
Total phosphorous	0.11	#
Lake width	0.11	n.s.
Lake area	0.1	n.s.
Nitrite	0.09	n.s.
Nitrate	0.1	n.s.
SECCHI depth	0.09	n.s.
Conductivity	0.08	n.s.
Ammonia	0.09	n.s.
Oxygen conc.	0.08	n.s.

Explanatory variables are ordered according to the order (lambda value) in forward selection.

** $p < 0.003$.* $p < 0.05$.

near significant.

were total-phosphorous, pH and water width. However not significant but other variables were also important such as ammonia, altitude and oxygen content. In case of emergent species, we found that altitude, pH, water depth and chlorophyll-a were the variables that explained significantly the differences in species composition. Other factors such as nitrogen forms (Kjeldahl-N, nitrite, nitrate), total-phosphorous, water width, area, oxygen content and SECCHI depth revealed as important but not significant variables.

Species communities were congruent among lake types. Only a few species appeared in a specific lake type. *Nymphaea alba*, *Nymphoides peltata*, *Stratiotes aloides* and *Trapa natans* observed in the left side of the plot (in MEDs); *Potamogeton perfoliatus* observed in the lower part of the plot (in BIGs), whereas *Chara* species were situated in the upper part of the plot (in ALKs). Species distribution was similar in emergent macrophytes; most of the species were observed in the centre of the plot. *Bolboschoenus maritimus* observed in the right side of the plot (in ALKs). *Carex distans*, *Euphorbia palustris* and *Glyceria fluitans* were situated in the lower part of the plot (in MARSHs), while *Petasites hybridus*, *Agrostis canina* and *Poa palustris* were observed in the left side of the plot (in ALKs).

4. Discussion

4.1. Macrophyte diversity of lakes

This study is the first which used diversity partitioning to evaluate the contribution of different habitat types to the regional diversity of macrophytes in the Pannon Ecoregion. The mean number of submersed species is comparable to the values found in other Ecoregions (Rørslett, 1991; Toivonen and Huttunen, 1995; Akasaka et al., 2010; Chappuis et al., 2014), but the number of emergent species is found to be greater, which may be explained by the intermediate-high nutrient conditions in the Pannon Ecoregion (VKKI, 2010b).

Compared with mean alpha, all habitat types had relatively low beta1 and low beta2 diversity values, indicating relatively small differences in species numbers both within and between lake types, at least compared with other aquatic groups, such as fish (Erős, 2007) or macroinvertebrates (Suurkuukka et al., 2012). These results emphasize the general uniformity of lakes in terms of species composition over the ecoregion.

Both Shannon and Simpson diversity indices indicated large differences between the submerged and emergent groups in the relative contribution of alpha and beta1 diversity to within lake type diversity. Beta1 diversity was especially high for emergent macrophytes irrespective of lake type, suggesting large differences in the abundance of common species between lakes. High beta1 diversity values also suggest environmental heterogeneity over the ecoregion, which might be explained by the pattern of environmental variables (Alahuhta and Heino, 2013) and not by dispersal-related processes (Alahuhta et al., 2013). On the other

hand, beta2 diversity of submerged and emergent macrophytes was found to be low. Overall, compared with the results on species richness, diversity indices showed a different picture on patterns in alpha and beta diversity, and revealed the role of species relative abundances. Due to the similar pattern of Simpson and Shannon diversities we can assume that rare species affect habitat diversity a little and consequently frequent species drive within and between habitat type diversity of macrophytes in the Pannon Ecoregion. Altogether, the results of diversity partitioning suggest that emergent macrophyte communities contributed the most to within and between lake type diversity and total (gamma) diversity.

The relatively small and shallow marsh habitats had a comparable level of diversity to medium lakes and big lake basins that is important from a conservation perspective. Current conservation efforts concentrate mainly on large lakes, while small lakes and ponds have less importance in habitat conservation. Our findings are thus in agreement with recent studies emphasizing the efficiency of conserving small wetlands (Davies et al., 2008), ponds (Williams et al., 2004; Cérégino et al., 2014) and temporary pools in agricultural landscapes (Lukács et al., 2013) and argue against the assumption of current ideas, which consider only large water bodies in environmental management and conservation (see the *Water Framework Directive, 2000/60/EC*).

Large shallow lakes and small-medium sized shallow lakes had similar alpha and beta diversity values. On the other hand, the diversity values of reservoirs were also comparable with that of natural lakes for all diversity components (alpha, beta and gamma) and indices (species richness, Shannon and Simpson). This finding is consistent with the observation of Chappuis et al. (2014) who found that Catalanian reservoirs maintain higher number of macrophyte species than ponds. Schmera and Baur (2011) found that macroinvertebrate diversity of artificial lowland and natural streams were almost identical in the Pannon Ecoregion. In fact, Schmera and Baur (2011) explained their results with a more abundant aquatic vegetation of artificial watercourses due to constant human perturbation. Dorotovičová (2013) explained the high macrophyte diversity of artificial watercourses in the Danube Basin with environmental heterogeneity. We can confirm that artificial reservoirs maintain similarly diverse emergent species communities as marshes and shallow lakes. Although, the purpose of reservoirs is to store water, our study reveals that they also support biodiversity contributing to the range of suitable habitats for macrophytes, and especially for emergent species.

The applied habitat classification scheme proved to be really effective in characterizing macrophyte communities in the Ecoregion. Alkali lakes differed the most from all lake types as implied by their low alpha diversity values and unique plant communities. Based on the uniqueness of vegetation, we suggest that conservation management should focus more on alkali lakes in the Ecoregion. Due to the arid continental climate, astatic (temporarily dried out) standing waters and fast organogenic succession with enhanced standing water succession are characteristic in the Pannon Ecoregion. Because of the astatic features of standing waters, emergent species are the main characteristic elements of lakes, which reflect the importance of the shoreline area in maintaining species diversity.

4.2. Environmental variables explaining aquatic macrophyte species distribution

Macrophyte communities reflect the physical conditions of lakes (Loughheed et al., 2001), as well as nutrient concentrations (Della Bella et al., 2008; Lukács et al., 2009), climatic and geological factors (De Catanzaro et al., 2009). The CCA analyses of different life-forms of macrophytes confirmed that different environmental

variables drive submerged and emergent macrophyte communities.

According to the first two axes, 68.4% of species–environment variance remained unexplained by local variables which may be due to some overlooked factors. Although, water column chemistry is the most important variable group in explaining aquatic macrophyte distribution; the remaining variance might be explained by e.g. sediment variables that were found to explain a large variance of macrophyte diversity in other studies (Chappuis et al., 2014). According to variable selection, we revealed that besides conductivity (=ionic contents), the lakes geomorphology (altitude, width, depth), the trophic state (=chlorophyll-a) and the plant nutrients (phosphorous and nitrogen forms) are the main environmental variables that determine submerged and emergent species distribution. Consequently, our results are in accordance with studies found that trophic status, ionic content, lake area, altitude (Vestergaard and Sand-Jensen, 2000; Capers et al., 2010; O'Hare et al., 2012) are the main drivers of macrophyte diversity in lakes.

We detected an inverse relationship between conductivity and Secchi transparency in both life forms of macrophytes. Low Secchi transparency is caused by wind action causing sediment resuspension in the waters in alkali lakes. Our findings reflect the importance of alkali lakes in the Ecoregion especially in case of emergent macrophytes. High water conductivity and low transparency was the main determinant of alkali lakes, which is mainly caused by the extremely high concentration of sodium bicarbonate. Such environmental conditions can only be tolerated by a few macrophyte species (e.g. *Potamogeton pectinatus* and *Bolboschoenus maritimus*), therefore these abiotic factors can be responsible for low diversity and habitat uniqueness of alkali lakes.

Morphology of lakes also influenced the type of macrophyte communities as high exposure can prevent the establishment of submersed macrophytes through disturbance of wave and wind actions (Keddy, 1985) in wide lakes such as large shallow lakes and some of the alkali lakes. We did not examine this factor directly in this study, but we suggest that wave and wind exposure would play an important role in shaping macrophyte communities in exposed habitats (Istvánovics et al., 2008; Janssen et al., 2014). Consistent with our results, numerous studies reported that submersed macrophyte communities could disappear by water turbidity (low Secchi transparency) because of light limitation (Ibelings et al., 2007). Lake morphology via lake depth is also responsible for the species poor submersed macrophyte communities of reservoirs.

There was a relatively low nitrogen content and high Secchi transparency in small-medium sized shallow lakes creating a suitable habitat for several rare and sensitive submersed species such as *Nymphaea alba*, *Riccia fluitans*, *Potamogeton natans*, and *Potamogeton lucens*. These results are similar to our previous findings in oxbow-lakes (Lukács et al., 2009, 2011).

Emergent macrophyte communities of shallow lakes and marshes did not differ in the CCA. Characteristic emergent species communities were found only in alkali lakes and reservoirs. It is likely that reservoir communities differed from other habitats because the studied reservoirs were located in the mountainous regions, and therefore they were characterized by emergent species which mostly appear along montane rivers and lakes such as *Poa palustris*, *Scirpus sylvaticus* and *Petasites hybridus*. According to the diversity analyses, marshes maintained similar diversity of submersed and emergent species to shallow lakes. CCA analyses revealed that macrophyte communities of marshes were more similar to small-medium sized shallow lakes and differed from large shallow lakes.

Some macrophytes showed narrow distribution range and were adapted for specific water conditions e.g. species of alkali lakes and reservoirs mentioned above. These species were located in the corner of CCA figures and were indicators of “extreme”

conditions (high salinity, clear water). On the other hand, most of the macrophytes were widespread, located in the centre of CCA figures and had no specific environmental demands. The IndVal analyses (see Electronic Appendix) complemented the results of the CCA analyses and confirmed that *Chara* species and *Carex pseudocyperus* were indicative specialists for BIGs, *Sparganium emersum* was an indicative specialist for RESs, *Equisetum palustre* and *Sagittaria sagittifolia* were indicative specialists for MEDs, while *Cirsium brachycephalum* was the only indicator specialists for MARSHs. Other species e.g. *Cicuta virosa*, *Allium angulosum*, *Leucojum aestivum*, *Urtica kioviensis*, *Ranunculus lingua* and *Senecio paludosus* were specialists without indicator value. All these specialists are generally considered as rare species in the Ecoregion. Contrary to our expectations, we found that lakes in the Pannon Ecoregion contain only a few numbers of alien species (*Typha laxmanni*, *Echinocystis lobata*, *Elodea canadensis*, *Solidago gigantea*; see Electronic Appendix). However, they might invade the buffer zone of lakes (meadows, forests, etc.) and invoke serious conservation problems.

Although we did not address directly in our study, but it is likely that dispersal processes and/or spatial autocorrelation with some unmeasured environmental variables may also influenced patterns in beta diversity between lake types. For example, spatial processes (i.e. dispersal, spatial autocorrelation see e.g. Dray et al., 2012) not affected beta diversity of macrophytes at large spatial scales and in case of relatively stable lakes (Alahuhta and Heino, 2013), whereas dispersal processes influenced the assemblage organization of macrophytes at smaller spatial scales in temporarily dynamic system of floodplain lakes (Padial et al., 2014). The spatial distribution of lakes differed markedly in our lake types, which may influenced patterns in their beta diversity values. Exploring how beta diversity changes in the function of spatial relationships between lakes in different lake types would be an important research avenue in the future to better understanding the regional scale diversity of macrophytes in ecoregions with a diverse array of lake types.

5. Conclusion

Both natural and artificial lakes are important elements of the landscape in strongly human modified regions, such as Central Europe. We showed that the diverse lake types of the Pannon Ecoregion were important for the conservation of freshwater biodiversity, harbouring a high number of macrophyte species (Lukács et al., 2009; Radulović et al., 2011). Our results support the importance of small lakes and artificial lakes in the conservation of macrophyte diversity compared to large and natural lakes as it was confirmed by the high diversity of both submersed and emergent species.

Due to their high alpha and beta diversity emergent macrophytes are the main characteristic elements of lakes in the Ecoregion, which reflect the importance of the shoreline area in typology and in ecosystem function as well as in habitat quality assessments. Most of the national assessment methods which use indicator species lists for the assessment of ecological status rely exclusively on submersed macrophyte species (Penning et al., 2008; Dudley et al., 2013; Kanninen et al., 2013; Alahuhta et al., 2014; Kolada, 2014; Kolada et al., 2014). We conclude that emergent macrophytes are decisive elements for lakes; hence ignoring these species during macrophyte surveys means that important ecological information may remain hidden.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.limno.2015.06.002>

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