Wetlands
DOI 10.1007/s13157-011-0182-7

ARTICLE

The Importance of Local and Regional Factors on the Vegetation of Created Wetlands in Central Europe

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Received: 1 July 2010 / Accepted: 29 April 2011

Abstract We assessed the relative importance of regional and local processes to wetland plant diversity in created depressional wetlands in Central Europe (Košské mokrade wetlands, central Slovakia). Twelve wetlands were sampled for vegetation, water chemistry, morphological, and hydrological data in 2008. A total of 39 plant species were found in the wetlands, dominated by *Typha latifolia* L. The results support the hypothesis that local environmental variables affect both species diversity and composition. Wetland plant diversity was negatively related to electrical conductivity, with a model significantly explaining 34.4 and 31.9% of the variance in species richness and Shannon diversity, respectively. Similarly, species composition was significantly related to local characteristics. A model relating species abundance data to local conditions explained 47.6% of the variation by age ("pure" effect=18.2%), water depth (15.1%), and conductivity (12.2%). Using measures of connectivity among wetlands, we did not find any significant relationships between plant communities and regional variables. Nevertheless, floristic data revealed significant small-scale (0–500 m) positive autocorrelation, indicating that wetlands in near proximity are more similar in species composition than more distant wetlands. This may suggest that the composition of nearby wetlands plays a role in shaping local communities.

Keywords Conductivity · Dispersal limitation · Macrophytes · Primary succession · Slovakia · Spatial analysis

Introduction

Wetlands are among the world's most sensitive habitats. They are delicately balanced with their environment and are affected by any change, however small, in the atmosphere, the water supply, or local land use (Moore 2006). Wetland plants are especially affected by many environmental factors as well as human impact (Lacoul and Freedman 2006). The beginning and subsequent development of wetland vegetation is characterised by the initial local conditions at the site and by subsequent events, including the availability of propagules, appropriate environmental conditions for germination, growth, and replacement by plants of the same or different species as site conditions change in response to both abiotic and biotic factors (Mitsch and Gosselink 2000). Thus, the species composi-

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tion at a given site is the result of both regional and local processes, where the role of chance in the development of communities is profound (Leibold et al. 2004; De Meester et al. 2005; Freestone and Inouye 2006). Species composition in habitat patches undergoing succession reflects both colonization, influenced by the position of the patch within the larger landscape, and population persistence, influenced by local environmental conditions within the patch (Botts 1997). At the regional scale, limits to dispersal frequently limit the rate of succession and introduces variation in species composition (Reinhartz and Warne 1993; Walker and del Moral 2003; Freestone and Inouye 2006). In some cases, dispersal problems may prevent some species from occurring even though local conditions for it are suitable (van der Valk 2006). On the other hand, local conditions at the site can preclude the establishment of species even if they are able to disperse there.

Among local factors, hydrology is crucial to the function of wetland systems (Reed 1993) and hydrological regime is one of the major factors influencing succession of wetland communities (Niering 1989; Fennessy et al. 1994). The hydroperiod may exert a strong impact on species sorting and selection gradients, and thus local variation in hydrological regimes may constitute an important predictor of species composition (Urban 2004; De Meester et al. 2005).

The area of global wetlands and their conditions are continually changing. Half of the total wetland area has already been lost and much of the remaining wetlands are degraded (Zedler and Kercher 2005). As this degradation and loss of wetlands have occurred, resource managers and organisations involved in nature conservation have recognized the need for wetland restoration and even the creation of new habitats (Biebighauser 2007; E.P.C.N 2007). However, even today degradation processes continue to be uncontrolled in many parts of Europe. As pointed out by Oertli et al. (2009), despite our greater awareness, basic knowledge of wetland biology and ecology is still full of gaps. Studies targeting wetland biodiversity are particularly important at the regional scale (e.g., Williams et al. 2003; Angélibert et al. 2006), but such studies are still scarce and there is urgent need for studies from many parts of Europe. Therefore, this study attempts to partly fill this void by addressing the problem of wetland plant biodiversity at different spatial scales in Central Europe.

The upper Nitra River Basin (central Slovakia) is a region that has been critically affected by past economic activities and associated environmental negligence (Drdoš and Székely 1994). After the Second World War, river regulation, intensive agriculture and industrial development all contributed to reducing the biological diversity of the landscape. Paradoxically, mining, which is the major industry of the region, has contributed greatly to recent increases in biodiversity. For example, extensive underground coal mining operations brought about changes to surface landforms and created a relatively dense pond system called Košské mokrade wetlands (Svitok et al. 2009). These wetlands occur in homogenous geomorphic settings in which particular wetlands appeared in a chronosequence linked to mining activities. Wetlands of several ages are in close juxtaposition, permitting the use of the space-for-time substitution approach (Pickett 1989) by studying successional changes in species composition. Moreover, these wetlands span a relatively broad range of ecological gradients in terms of morphology, hydrological regime, and nutrient concentrations. This allows the study of associations between floristic characteristics and these gradients.

Here, the relative importance of regional (spatial) and local processes to wetland plant communities is assessed based on the observed distribution of species in natural conditions. More specifically, two main hypotheses were evaluated: 1) The "local hypothesis" suggesting that inter-annual variability in wetland size, wetland age, and other locally specific variables are the primary factors shaping wetland communities; and 2) the "regional hypothesis" suggesting that limits to dispersal influence species composition in a naturally patchy system, and wetlands close to each other are more similar than distant ones. Subsequently, the study integrates locally specific variables and the spatial configuration of wetlands in order to identify the relative contributions of both local and regional processes to the variation in macrophyte community composition.

Study Area

The studied wetlands are located in the upper Nitra River Basin (central Slovakia), south of the town of Prievidza, near the prior site of the village Koš that was relocated due to mining activities (Fig. 1). The climate of the area is cool and moderately humid (altitude 246–273 m, mean annual air temperature 8–9°C, mean annual precipitation totals 600–700 mm, Miklós 2002). The actual temperature and precipitation in the year of study were 10.8°C and 655 mm, respectively (Slovak Hydrometeorological Institute).

The origin of Košské mokrade wetlands is related to underground coal mining that resulted in changes to surface landforms. The first flooded terrain depressions filled by underground or rainfall water appeared in 1986 and quickly became a "hot spot" for regional biodiversity (Svitok et al. 2009). A substantial part of the wetland system occurred within an agricultural landscape with barley, wheat, and corn as the most common crops.

In total, 12 wetlands were randomly chosen for the survey presented here, with total area of about 20 ha. The

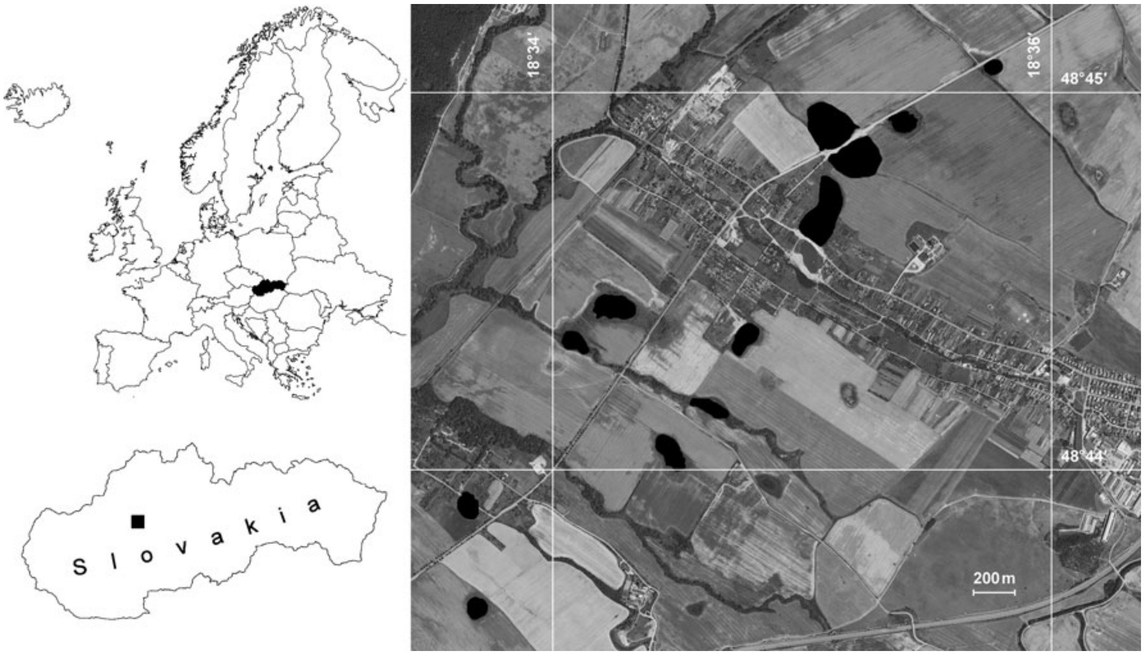

Fig. 1 Map of the Košské mokrade wetlands in the upper Nitra River Basin. The wetlands surveyed in 2008 are identified by black colour

wetlands occur in homogenous geological conditions of claystones and sandstones covered by quaternary floodplain sediments (Miklós 2002). The bottom substrate at all investigated wetlands consisted of fine (silt/clay) sediment, with a homogeneous composition across the sites (cf. Willby et al. 2000). The study sites incorporate a range of environmental conditions including hydrology, morphology, chemistry and age; basic wetlands characteristics are provided in Table 1.

Methods

Field research was carried out in July 2008. Within every studied wetland, all macrophytes (bryophytes, vascular plants, macroscopic algae and Algae filamentous group) were sampled using a five level scale ("Plant Mass Estimate"; 1—rare, 2—occasional, 3—frequent, 4—abundant, 5—very abundant, Kohler 1978; Kohler and Janauer 1995). Because the surveyed wetland areas were relatively small, an exhaustive estimation of plant mass was feasible and thus plot-level sampling was not employed. Data were collected from hydro- and littoral ecophases (*sensu* Hejný 1960). The nomenclature of both non-vascular and vascular plants follows Marhold and Hindák (1998).

Those environmental variables that were hypothesised to determine the distribution of macrophytes were measured in each study wetland (Table 1). To minimize temporal variability, all water samples were taken during the morning hours on 1 day. Within each wetland, one composite water sample was taken from open water areas, consisting of at least five sub-samples that were collected randomly from different locations. Physicochemical characteristics such as water pH and electrical conductivity (25°C) were measured in the field using a WTW pH/Cond 340i. For analysis of ammonia, nitrite, nitrate, and phosphate levels, the water samples were quickly frozen and maintained at −18°C until measurement. Ammonia content was determined by an ion-selective electrode at 20°C. Nitrite content was determined spectrophotometricaly at $\lambda=540$ nm, after diazotation with 40 g/l sulfanilamide and 2 g/lN-(1-naphthyl)-ethylenediamine dihydrochloride in 10% H_3PO_4. Nitrate plus nitrite was measured by the same method except that the samples were reduced with 1.4 g/l hydrazinsulphate, 7.5 g/l $CuSO_4$ and then neutralised by adding 3 g/l NaOH a prior to the diazotation. The nitrate content was then calculated as the difference in the absorbance of the same sample with and without reduction. If the nitrate content in the sample was above 0.1 mg/l, its level was checked using an ion-selective electrode at 20°C. The phosphate content in the samples was analyzed spectrophotometrically according to the modified method described by Chen et al. (1956), measuring the absorbance of the samples at $\lambda=720$ nm after derivatization with ammonium-molybdate reagent containing 0.1 M sulfamic acid, 0.01 M ammonium molybdate, 0.1 M potassium antimonyl oxide tartarate and 0.1 M ascorbic acid.

Water depth was measured from a boat at six points positioned proportionally along a transect through the longest dimension of each of the wetlands. The percentage cover of trees and shrubs along wetland banks was obtained from an orthophoto map. The inter-annual hydrological

Table 1 Summary of environmental characteristics of the Košské mokrade wetlands

Characteristics	Mean	SD	Min	Max
Local				
Electrical conductivity (µS/cm)	507	416	110	1714
pH	8.7	0.29	8.4	9.5
NH_4^+ (mg/l)	1.98	3.90	0.35	14.26
NO_3^- (mg/l)	2.29	2.19	0.93	9.13
NO_2^- (mg/l)	0.20	0.14	0.03	0.46
PO_4^{3+} (mg/l)	1.40	1.01	0.21	3.52
Total area of open water (ha)	1.74	1.33	0.49	4.42
Average depth of water (cm)	184	218	50	783
Maximum depth of water (cm)	283	336	50	1100
Riparian vegetation cover (%)	24	29	0	95
Age of wetland (year)	12	4.6	5	22
Year-to-year variability in size (% CV)	41.4	8.3	24.8	92.5
Regional				
Distance to nearest wetland (m)	202	145	20	415
Connectivity within 250 m	1.3	1.2	0	3
Connectivity within 500 m	2.3	1.2	1	4
Connectivity within 1,000 m	6.1	1.7	3	9
Distance to nearest stream (m)	686	271	150	1080

regime was expressed as the between-year coefficient of variation (% CV) of wetland size, which was calculated from 12 years of available data (1997–2008). Information on the age of wetlands was derived from GIS models and the schedule of mining activities under the respective wetland. The maps and GIS models, kindly provided by the mining company (Hornonitrianske bane Prievidza, a.s.) and based on mandatory periodical surveys, provided a well documented history of temporal and spatial dynamics of the wetlands, and gave data on the total area of each wetland.

The distance to the nearest wetland and the distance to the nearest stream were extracted from digitized maps. In order to assess habitat connectivity, the number of wetlands present within a 250, 500, and 1,000 m radius was derived using GIS data layers.

Data Analysis

Species Composition

Data on the species compositions were summarized for the wetlands using species-incidence and abundance matrices. Both kinds of composition matrices were used in the analyses to help understand how much the species response was driven by compositional differences and how much was driven by differences in relative abundances (cf. Anderson et al. 2006; Heino 2008). Rare species found at only a single wetland were deleted from the original data matrices to improve the signal-to-noise ratio (Gauch 1982). Widely used traditional multivariate techniques are not always appropriate for the analysis of species data (Legendre and Legendre 1998; Legendre and Anderson 1999; Legendre and Gallagher 2001), and thus we employed multivariate methods based on measures of ecological distance (dissimilarity). The distance matrices were constructed using dissimilarity measures described by Sørensen (1948) and Bray and Curtis (1957) that are ecologically relevant (Faith et al. 1987).

At the first stage, similarity of the floristic composition of particular wetlands was visualized using principal coordinate analysis (PCoA, Gower 1966). The obtained coordinates were submitted to *k*-means partitioning (Legendre and Legendre 1998) in order to classify wetlands according to their plant species composition, i.e., to delimit distinct groups. This non-hierarchical clustering method rearranges objects into an *a priori* specified number of groups (*k*), while trying to find groupings with the minimum sum (over all groups) of the squared within-group residuals. The procedure was repeated 1,000 times with a random starting allocation of wetlands into groups. The C-H pseudo-F statistic (Caliński and Harabasz 1974) and the sum of significant indicator values (see below) were used as criteria for choosing an optimal clustering solution. To facilitate the interpretation of ordinations, 95% confidence ellipses (Murdoch and Chow 1996) based on the standard deviations of site scores were calculated for each community type as defined by *k*-means partitioning and displayed in the ordination plots. Species characteristic for a particular group were identified using indicator species analysis (Dufrêne and Legendre 1997). Classical indicator species analysis was conducted for abundances, and a simplified version was used for incidence data. The indicator value (IndVal) of each species was tested using 9999 permutations. The species with high IndVal (>60%) were regarded as characteristic indicator species for the group in question. Scores of those species were added into ordinations as weighted sums of particular composition matrices.

Stepwise distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999; McArdle and Anderson 2001) accompanied by appropriate permutation tests (9999 permutations) was performed to address the hypotheses concerning local and regional variables. Prior to the analyses, distributions of the environmental data (Table 1) were examined, and some variables were either logarithmically (total area, average depth), reciprocally (ammonium, nitrate), or arc-sine square root transformed (bank vegetation cover) to make their distributions more symmetric and to reduce the effect of potential outliers. The variable pH was excluded from the analysis because of the presence of a strong outlier (9.5) but otherwise biologically insignificant variability (pH range: 8.4–8.8).

At the next stage, correlated variables (Pearson correlation $r>0.7$) were identified to avoid the problem of multicollinearity. An iterative forward selection procedure was used to build parsimonious models. Separate models were built for local and regional data. Only those variables with the conditional effect significant at $p<0.05$ were retained in the models. At each iteration, a different subset of uncorrelated variables entered the forward selection, giving different parsimonious models. Among those models, the model that best explained the variation in the species data matrix was regarded as the final model. In addition, a variation partitioning procedure (Borcard et al. 1992) was applied to distinguish the relative importance of particular variables to the wetland communities.

The spatial patterns in macrophyte communities were further evaluated by multivariate correlograms (Oden and Sokal 1986) where the normalized Mantel statistic r_M (Mantel 1967) quantified autocorrelation. The geographical distances between wetland pairs were partitioned to four equidistant classes lagged by 500 m. Mantel statistics for the larger distance classes were not considered in the correlograms because they were based on just a small number of wetland pairs. Each value of r_M was tested for significance using permutation tests (9999 permutations). Significance levels were adjusted for multiple testing using progressive Bonferroni correction (Legendre and Legendre 1998).

Diversity

Species diversity was quantified as species richness and Shannon diversity (Shannon and Weaver 1949). Because of possible species-area effects, the relationship between diversity measures and sampling site area was assessed in the first step of the analysis. Neither species richness ($r=-0.09$) nor Shannon diversity ($r=-0.11$) showed significant correlation with wetland area.

Analogous to the multivariate analyses, stepwise multiple regression analysis was performed to test the hypotheses on diversity measures. Because of the intrinsically small sample size ($n=12$), a permutation counterpart of the F test (9999 permutations) was employed to ensure that non-normality did not affect the results. The final models were chosen from several parsimonious models as those with the smallest estimated residual sum of squares based on the leave-one-out cross-validation procedure (Roff 2006). The quality of the models was carefully checked at each step using residual diagnostic plots.

Results

Species Composition and Diversity

A total of 39 plant species (1—macroscopic algae, 1 bryophyte, and 37 vascular plants), plus filamentous algae as a group, were identified. Of these, six were found at half or more of the sites. *Typha latifolia* was the most widespread species and was found at all sites (100% occurrence frequency), followed by *Lycopus europaeus* (83%), *Lemna minor* (83%), *Alisma plantago-aquatica* (67%), *Juncus effusus* (50%), and *Rumex maritimus* (50%). Fourteen species were considered rare, with occurrence in only one wetland. Almost 72% of the species are helophytes, more than 20% hydrophytes, and almost 8% amphiphytes. According to the Plant Mass Estimate, *T. latifolia* and *Potamogeton pusillus* were abundant species in some wetlands. Plant species richness ranged from 5 to 13 species per wetland, and the Shannon index ranged from 1.46 to 2.47 (excluding rare species).

Plant Responses to Environmental Variables

Regardless of the diversity measure used, multiple linear regression analyses of local variables resulted in models that retained electrical conductivity as the single best predictor of plant species diversity. Species richness ($F_{1,10}=5.26$, $P=0.039$) and Shannon diversity ($F_{1,10}=4.69$, $P=0.0495$) decreased with increasing conductivity (Fig. 2). Within this broad trend, however, a group of wetlands with intermediate conductivity (400–600 µS/cm had a considerably high dispersion of diversity values resulting in relatively low determination coefficients. Electrical conductivity explained 34.4 and 31.9% of the variance in species richness and Shannon diversity, respectively. The regression analyses showed no significant relationships between diversity measures and the remaining local and regional variables.

The Sørensen index of similarity ranged from 0.15 to 0.67 (mean=0.45), and the Bray-Curtis similarity (aka Steinhaus index) from 0.26 to 0.7 (mean=0.44) among pairs of wetlands, indicating a relatively diverse mosaic of communities. The best clustering solution for the presence/absence data revealed two distinct groups of wetlands (Fig. 3a). The first coordinate was strongly correlated with age ($r=-0.85$) and clearly separated the older (mean age=21 years) and the younger wetlands (mean age=11 years). Indicator species analysis identified *Rorippa palustris*, filamentous algae, and *Alisma plantago-aquatica* as characteristic taxa for the older wetlands (Table 2). In contrast, *Lycopus europaeus*, *Lemna minor,* and *Juncus effusus* were characteristic of younger wetlands. The variation in wetland scores for the first principal coordinate was also significantly related to ammonium ($r=-0.70$) and nitrate ($r=-0.61$) concentrations, both of which were also positively correlated with wetland age (ammonium $r=0.72$, nitrate $r=0.63$). The average concentration of ammonium was 11 times higher in older than in younger wetlands, and the average nitrate concentration was three times higher in older than younger wetlands.

A similar pattern was seen in the PCoA regarding quantitative information (Fig. 3b). Moreover, abundance data allowed us to distinguish communities of deep (mean depth>3 m) and shallow (mean depth<1 m) young wetlands, which were separated along the second coordinate that was correlated with depth ($r=0.68$). The abundance values of *Lemna minor* and *Alopecurus aequalis* were higher in shallow wetlands while values of *Lycopus europaeus* and *Najas marina* were higher in deep wetlands (Table 2).

The PCoA findings were supported by the direct ordination. Db-RDA on the presence/absence data identified wetland age as the single best predictor (pseudo-F= 4.03, $P<0.001$), explaining 28.7% of variation in species presence/absence data. When the abundances of species were considered, the most parsimonious model with the highest explanatory power included wetland age, average depth and electrical conductivity (pseudo-F=2.42, $P<0.001$). The final model explained 47.6% of the variation in species data. Of that, 18.2% can be explained solely by age, 15.1% by depth, and 12.2% by conductivity. The remaining 2.2% of species variation was accounted for by joint effects of the local variables in question, as assessed by using a series of partial db-RDAs. The regional variables did not show any significant relationship with species composition.

Spatial Patterns in Species Composition

The spatial structure of species composition was interpreted from Mantel correlograms (Fig. 4). The correlogram based on abundance data (Fig. 4b) was globally significant at the Bonferroni corrected level $\alpha'=0.013$. Small-scale positive autocorrelation (0–500 m class in the correlogram) suggests that plant species composition from pairs of wetlands close to each other are more similar than expected for randomly associated pairs. In contrast, the negative significant value found at distance class 1,000–1,500 m suggests that the species composition of more distant wetlands is less similar than expected by chance alone. A further increase in standardized Mantel r may have indicated some degree of patchiness in species composition. However, an interpretation of autocorrelation coefficients was prevented by the lack of wetland pairs at these greater distances. The correlogram based on presence/absence data revealed a similar pattern (Fig. 4a), but the values of r_M for the first and third distance classes remained marginally non-significant (progressive Bonferroni corrected $P=0.060$ and $P=0.051$, respectively).

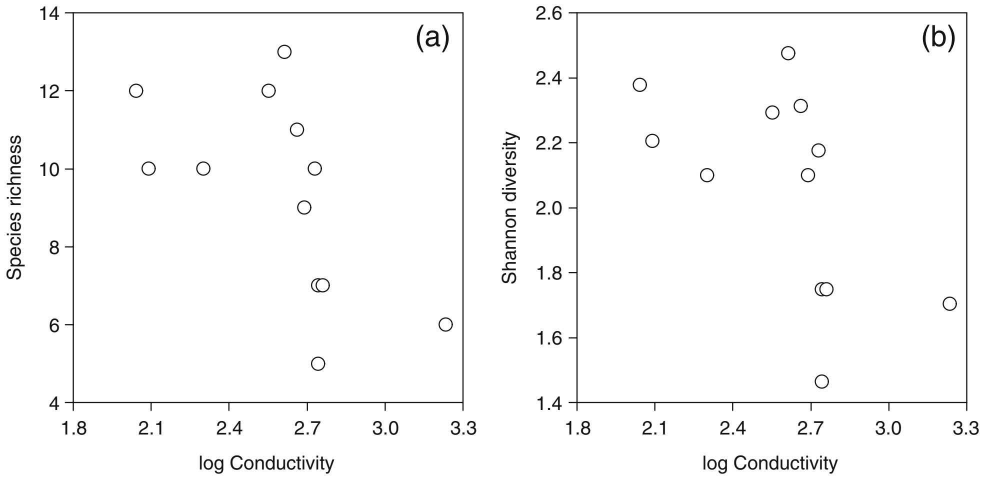

Fig. 2 Relationship between plant species richness (**a**), Shannon diversity (**b**) and electrical conductivity (log transformed) at the Košské mokrade wetlands

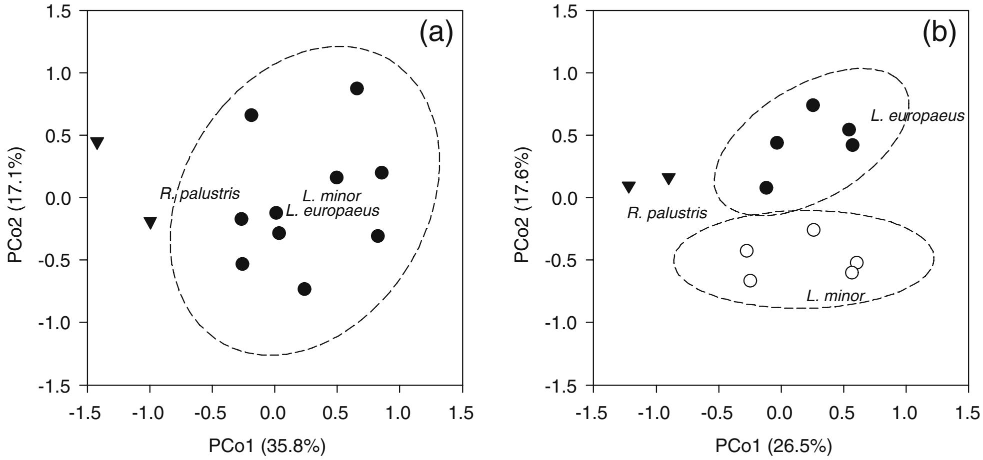

Fig. 3 PCoA ordination of plant species data based on Sørensen (**a**) and Bray-Curtis (**b**) dissimilarity measures. The variations explained by the first two coordinates are given. Distinct groups of wetlands, according to the *k*-means partitioning, are displayed using different symbols: *triangles*—old wetlands, *circles*—young wetlands. The *empty* and *solid circles* differentiate shallow and deep younger wetlands in the Bray-Curtis PCoA. Ninety-five percent confidence ellipses are shown for the groups delineated by cluster analysis. No ellipse is shown for the old wetlands because the group consisted of only two wetlands. Scores of significant indicator species for each group are superimposed

Discussion

Species Composition and Diversity

The species composition of Košské mokrade wetlands was dominated by the cattail *Typha latifolia*, a clonal perennial species that appears soon after disturbances in moist or wet habitats or occurs early in the primary succession of open water (Reinhartz and Warne 1993; Atkinson et al. 2005). Cattail is a superior competitor (C strategy) in wetlands with undisturbed and fertile habitats (Wisheu and Keddy 1992) and is considered a good indicator of eutrophication (Khan and Ansari 2005). The presence of other helophyte species was limited to gaps (e.g., *Bolboschoenus maritimus* s. lat.) and less dense cattail canopies (e.g., *Lycopus europaeus* or *Juncus effusus*). This exclusion of other species by *T. latifolia* monocultures is well known (Odum 1988). Locally abundant helophytes such as the water plantain (*Alisma plantago-aquatica*) and golden dock (*Rumex maritimus*) were restricted to shallow wetland edges or exposed bottom substrates. These and some other species of wide ecological amplitude (*Bidens frondosa*, *Ranunculus sceleratus*, *Rorippa palustris*) are able to quickly occupy new niches, especially in nutrient-rich habitats (Köck 1988; Moravcová et al. 2001; Klimešová et al. 2004; Šumberová et al. 2006).

The species diversity of hydrophytes was generally low, which is typical for the colder Carpathian bioregion of Slovakia where these wetlands occur (Hrivnák et al. 2009).

Table 2 Characteristic species for different wetland types based on the classification of presence/absence (qualitative) and abundance (quantitative) data. The wetland type column indicates the group for which the species is an indicator. Simplified and classical indicator values (IndVal) are displayed with corresponding probability values

Species	Wetland type	IndVal (%)	p (9999 permutations)
Qualitative classification			
Rorippa palustris (L.) Besser	old	91	0.046
filamentous algae	old	83	0.092
Alisma plantago-aquatica L.	old	63	0.516
Lycopus europaeus L.	young	100	0.017
Lemna minor L.	young	90	0.047
Juncus effusus L.	young	60	0.459
Quantitative classification			
Rorippa palustris (L.) Besser	old	88	0.030
filamentous algae	old	79	0.064
Lemna minor L.	young-shallow	64	0.026
Alopecurus aequalis Sobol.	young-shallow	60	0.141
Lycopus europaeus L.	young-deep	63	0.004
Najas marina L.	young-deep	60	0.132

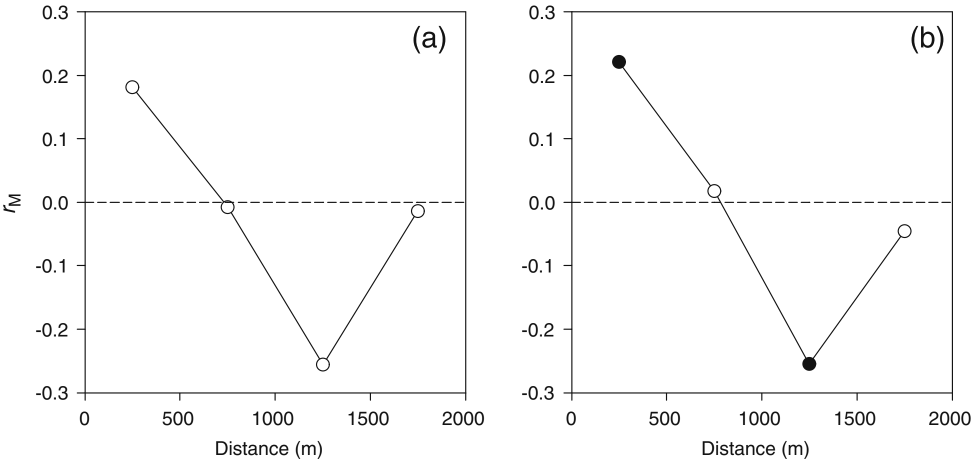

Fig. 4 Mantel correlograms of species composition based on Sørensen (**a**) and Bray-Curtis (**b**) dissimilarity measures. Distance classes were defined at 500 m intervals. *Black circles* represent normalized Mantel statistics (r_M) significant at α= 0.05

Among them, *Lemna minor*, *Najas marina*, and *Potamogeton pusillus* occurred more frequently, typically inhabiting shallow, eutrophic waters with fine sediments, according to expectations (Willby et al. 2000). Higher hydrophyte diversity is probably limited by the elevated trophic state of the wetlands (Penning et al. 2008) and climatic constrains. The warmer Pannonian bioregion in southern Slovakia is more suitable for the development of true aquatic plants and their communities than the colder Carpathian counterpart studied here (Valachovič et al. 1995; Oťaheľová and Oťaheľ 2006).

Plant Responses to Environmental Variables

Our results support the hypothesis that site-specific environmental variables affect both species diversity and composition. Plant diversity decreased as conductivity increased. Similar results were observed by Herault and Thoen (2009), who found a negative association of hydrophyte species richness with electrical conductivity within isolated closed depressions in open landscapes in Central-Western Europe. However, the relationship between wetland plant diversity and poor-rich gradient as measured by conductivity depends on the gradient range. For example, studies investigating wetlands in the lower part of the gradient might show an increased response in richness (Mäkelä et al. 2004; Biggs et al. 2005), whereas a decreased response might be observed at higher conductivities (Herault and Thoen 2009; present study). This may represent the initial rise and subsequent fall of diversity along the gradient, as predicted by the unimodal model of Grime (Grime 1973; Johnson and Leopold 1994).

The other local-scale factors of area, year-to-year variability in wetland size and nutrients did not show any significant relationships to plant diversity. This reflects either their homogeneous nature and lack of variability across the wetlands (nitrite, phosphate) or relatively low importance to plant diversity (area, depth). As argued by Edvardsen and Økland (2006), pond area is a poor predictor of aquatic species diversity because most species occur along the shallower pond margins, and the addition of a larger area with deeper waters and bottom sediments unsuited for colonisation by vascular plants has negligible effects on species richness.

The Košské mokrade wetlands are scattered across a homogenous agricultural landscape in a chronosequence spanning 5 to 22 years old, and thus patterns of successional changes in diversity were expected. However, no significant relationships were found between plant diversity and wetland age. The lack of any relationship between diversity and age is likely to reflect the rapid development typical for habitats such as wetlands with low stress and high productivity (Walker and del Moral 2003), especially if the propagule source is unrestricted (Mitch et al. 2005). If initial colonization or succession phases occur very quickly, then all of the major changes in diversity may have happened within the first few years and be missed by later surveys. For example, Odland (1997) reported rapid successional development in newly-created wetlands where the main vegetational change occurred between the third and the fourth year and the major changes in floristic diversity took place during the first 9 years since construction.

In contrast to diversity measures, the main compositional gradient was related to wetland age regardless of whether it was derived from quantitative or qualitative species data. This importance of age is in accordance with the results of other wetland studies conducted (Odland 1997; Odland and del Moral 2002). The presence of six taxa was associated with wetland age: Filamentous algae, *Rorippa palustris* and *Alisma plantago-aquatica* were found more often at older wetlands, whereas *Lycopus europaeus, Lemna minor* and *Juncus effusus* were characteristic for young wetlands. Paradoxically, a significant indicator of older wetlands, *R. palustris*, is regarded as a pioneer wetland herb (Klimešová et al. 2007), whereas *L. minor,* an indicator of young wetlands, is considered a eutrophic species typical for advanced stages of succession (Bornette et al. 1994). However, these results are rather difficult to explain within the framework of succession. In this context, the dichotomy between annuals and perennials is often used as a tool to understanding the rate of succession changes (van der Valk 1981; Matthews and Endress 2010). However, neither diversity nor abundance of perennial or annual guilds showed any significant relationship with age at the Košské mokrade wetlands. Moreover, almost all indicator vascular plant species, regardless of wetland age, could be classified as perennials. This suggests, as with diversity patterns, that early primary succession phases occurs quickly and the main shift in dominance of annual and perennial life histories happen within the first few years. Matthews and Endress (2010) showed that wetlands in agricultural landscapes underwent succession more rapidly, as indicated by a rapid increase in dominance by late-successional plants. The rapid establishment and development of vegetation has also been reported elsewhere (Odland 1997; Odland and del Moral 2002).

On the other hand, classification of species according to life span may not be always helpful in describing successional changes. For example, DeBerry and Perry (2004) found that the establishment of species did not follow the typical model of primary succession, which predicts an overall dominance of annual species with an exploitative advantage in new habitats. They suggest that certain wetland perennials utilize annual strategies when substrates are available. Similarly, short-lived pioneer species producing numerous seeds and forming a permanent seedbank, such as *R. palustris*, may be able to regenerate vegetatively from adventitious buds and resprout from root fragments, as is typical for perennial species (Klimešová et al. 2008).

Indeed, age-related differences in vegetation composition are not simply the result of life-span, propagule longevity or establishment characteristics, but likely reflect a mixture of biological and environmental factors changing with time. In the Košské mokrade wetlands, wetland age was positively correlated with ammonium and nitrates, with the average concentration of these nutrients several times higher in older than younger wetlands. The observed shift from duckweed (*L. minor*) dominance in young wetlands to filamentous algae in old wetlands seems to probably correspond with wetland nutrient status. In general, succession theory predicts that organic matter storage and nutrient cycles change over time as an ecosystem develops (Odum 1969; Craft et al. 1999). Thus, changes in nutrient status may reflect the maturation of wetlands, although we are not able to show causation because nutrient levels in water and sediment are not necessarily correlated (Houlahan and Findlay 2004).

When we considered quantitative information (species abundances), depth and conductivity emerged, in addition to wetland age, as significant predictors of species composition. In accordance with these results, Herault and Thoen (2009) found that electrical conductivity was an important predictor of plant assemblages in isolated depressional wetlands. The role of conductivity in determining plant species composition has also been reported for other types of wetlands (Toivonen and Huttunen 1995; Heegaard et al. 2001; Rolon et al. 2008).

Our comparison of shallow and deep wetlands revealed differences in species composition. While shallow habitats were characterised by an increased number of *L. minor* and *Alopecurus aequalis*, deeper wetlands typically supported higher abundances of *Lycopus europaeus* and *Najas marina*. These differences can be partially explained by the ecological requirements of these species in relation to water level fluctuations, the degree of flooding, and habitat desiccation (Hejný 1960; Willby et al. 2000; Sanderson et al. 2008). As in our study, water depth has often been used as a surrogate for hydrological regime in wetlands (Mitsch and Gosselink 2000; van der Valk 2006), with shallow wetlands more prone to desiccation than deeper ones. Local variation in hydrological regimes is an important driving force in the development of wetland vegetation, and may be a prominent predictor of species composition through the environmental filter of hydroperiod (Urban 2004; Wilcox 2004; De Meester et al. 2005; Wilcox and Nichols 2008).

Between-year variation in wetland size, as a proxy for the inter-annual hydrological regime, did not show any significant relationship with either plant diversity or composition. Inter-annual variability in wetland sizes ranged relatively widely among the sites (CV: 25–93%) but a closer examination of the data shows that almost all of the depressions were stabilised and did not substantially change their area already a few years before the floristic field survey was conducted. Thus, the flooding of new terrestrial areas followed by primary succession of wetlands was halted by stabilisation of the surface subsidence. The results from this analysis, consistent with other results described previously, would suggest a rapid and convergent development of vegetation in the Košské mokrade wetlands.

Spatial Patterns in Species Composition

The spatial analysis of floristic data from the Košské mokrade wetlands revealed a small-scale positive autocorrelation indicating that wetlands in near proximity are more similar in species composition than more distant wetlands. This suggests limits to dispersal where the wetlands represent spatially isolated habitat patches and the composition of nearby wetlands plays an important role in shaping local communities. That was expected, because the position of a habitat within a landscape usually influences rates of colonization and dispersal among habitat patches and introduces variation in species composition, even though the physical environment of the sites is similar (Walker and del Moral 2003; del Moral et al. 2005; Freestone and Inouye 2006). Thus, distance to the nearest seed source can have a strong effect on the number of native wetland species present at a particular site (Reinhartz and Warne 1993). As has been documented by Brown (1998), new wetland habitats located in proximity to adjacent wetlands have shown greater colonization than more remote sites. In the context of succession, geographical distance may limit the rate of succession, and sites near a source of potential colonists usually develop more rapidly than do isolated sites (Walker and del Moral 2003). The regional factors such as proximity of seed sources can be especially important in the early phases of succession when community development is determined as much by chance and landscape context as by the characteristics of the site itself (del Moral et al. 2005).

On the other hand, observed spatial patterns may arise for a number of other reasons. The Košské mokrade wetlands appeared non-randomly in the landscape as a consequence of underground mining activities which is in itself non-random process. As pointed out by Botts (1997), position of a habitat patch is often correlated with patch age in landscapes where new patches form sequentially. An additional spatial analysis of local variables (results not shown) revealed identical correlogram patterns for wetland age as those found for species composition. This suggests a clustering of wetlands of similar age in space. Consequently, the interpretation of relative importance of local and regional processes is not unambiguous due to the correlation of space and time.

The results of this study demonstrate the rapid development of vegetation in depressional wetlands within an agricultural landscape. In addition to successional changes, average depth of water and conductivity emerged as the most important factors shaping diversity and species composition.

Acknowledgment We are grateful for critical reviews and language correction of an early version of the manuscript by M. Novikmec and D. W. Hardekopf. This study was supported by the Scientific Grant Agency of the Ministry of Education and the Slovak Academy of Sciences (VEGA grant numbers 2/0013/08 and 1/0529/09).

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