Testing floristic and environmental differentiation of rich fens on the Bohemian Massif

Testování floristické a ekologické diferenciace bohatých slatinišť v Českém masivu

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The south-eastern part of the Bohemian Massif (the Bohemian-Moravian Highlands, the Třeboň basin, Czech Republic) is an important hotspot of fen biodiversity. Especially rich fens with calcium-tolerant peat mosses (the *Sphagno warnstorfii-Tomentypnion* alliance) currently harbour highly endangered organisms. In this study we gathered phytosociological and environmental (water chemistry, water table depth) data from 57 unique and well-preserved fens. The ISOPAM algorithm reproduced the expert-based classification at the alliance level presented in the Vegetation of the Czech Republic monograph. Particular types of vegetation were nearly completely differentiated in the PCA of environmental data and all their pairs differed significantly with respect to pH, which together with calcium was correlated with the major vegetation gradient. The secondary gradient coincided with the concentration of nitrate and potassium, but was not apparent in the bryophyte subset. When only data for vascular plants were analyzed, the major gradient reflected increasing number of species from poor to extremely-rich fens, including ubiquitous grassland species, and only partially coincided with pH and calcium. Contrary to expectations, neither the extremely rich or rich fens were associated with low concentration phosphorus in the water. In addition, particular vegetation types did not differ in the N:P ratio of bryophyte biomass. Species composition of extremely rich fens thus seemed to be determined predominantly by a high pH/calcium level and waterlogging, low iron concentration and absence of sphagna that would hamper regeneration of some competitively weak vascular plants. We demonstrated that the delimitation of the major vegetation types (alliances) along the poor-rich gradient makes great floristic and ecological sense also in the Hercynian Mountains and that pH and calcium rather than nutrient availability differentiate causally major vegetation types by determining structure of the moss layer.

Keywords: Bohemian-Moravian Highlands, bryophytes, classification, gradients, ISOPAM, mire, Třeboň basin, vegetation

Introduction

Fens (minerotrophic mires of the *Scheuchzerio palustris-Caricetea nigrae* Tüxen 1937 class) are remarkable habitats with a specific species composition. In central Europe they are among the most endangered habitats, hosting a large number of ecological specialists and rare species of different taxonomic groups (Grootjans et al. 2005, Poulíčková et al. 2005, Schenková et al. 2012, Hettenbergerová et al. 2013). Their botanical and zoological species compositions vary predominantly along a complex gradient of pH, calcium and total mineral richness, usually called the "poor-rich gradient" (du Rietz 1949, Sjörs 1952, Fransson 1972, Malmer 1986, Tahvanainen 2004, Hájek et al. 2006, Conradi & Friedmann 2013). The old ecophysiological premise that mineral-rich soils are also richer in nitrogen, phosphorus and potassium was abandoned, because in fens the gradients of increasing N, P and K availabilities can be largely independent of the pH/calcium gradient or may even correlate with pH negatively (Waughmann 1980, Wheeler & Proctor 2000, Bragazza & Gerdol 2002, Bragazza et al. 2005, Rozbrojová & Hájek 2008, Kooijman & Hedenäs 2009). On the other hand, either an over supply or a deficiency of a particular element may underlie the observed poor-rich vegetation gradient. Productivity of the most calcium-rich fens is strongly limited by phosphorus that is immobilized by calcium into forms unavailable to plants (Boyer & Wheeler 1989, Bedford et al. 1999). Some authors (Paulissen et al. 2004, Kooijman & Hedenäs 2009) further stress the importance of particular forms of nitrogen (ammonium versus nitrate) whose ratio may change along a pH gradient. Assessment of changes in nutrient availability along a poor-rich gradient is however difficult because of great seasonal variation in macronutrient concentrations in water (Hájek & Hekera 2004, Jiroušek et al. 2013). The alternative way of assessing the nature of nutrient limitation, plant stoichiometry (Güsewell & Koerselman 2002, Olde Venterink et al. 2003, Rozbrojová & Hájek 2008, Pawlikowski et al. 2013), is on the other hand affected by differences in element concentrations among the species (Malmer et al. 1992, Wojtuń 1994, Bombonato et al. 2010). In addition, some other factors apart from pH/calcium level and macronutrient availability may contribute somehow to forming the main vegetation gradients, such as, among others, water table depth and its dynamics (Bragazza & Gerdol 1996, Jabłońska et al. 2011, Schenková et al. 2014), iron toxicity (Rozbrojová & Hájek 2008, Aggenbach et al. 2013) or historical-biogeographical factors (Nekola 1999, Hájek et al. 2011b, Jiménez-Alfaro et al. 2012). The relationships between nutrient availabilities and species composition of fen vegetation are therefore not definitively resolved and studies from other than traditionally explored regions, especially those that display specific patterns of water chemistry, are needed. Understanding these relationships is a prerequisite of better conservation of endangered fen species in agriculture landscapes where high nutrient input seriously threatens persisting fen remnants (Zechmeister et al. 2002, Navrátilová et al. 2006, Koch & Jurasinski 2014).

In the boreal zone of Europe there have been numerous studies testing the importance of particular environmental factors for the species composition of fen communities (Persson 1962, Mörnsjö 1969, Malmer 1986, Heikkilä 1987, Sjörs & Gunnarsson 2002) and the same holds true for North America (Vitt & Chee 1990, Anderson & Davis 1997, Nekola 2004). In central Europe, the relationship between environmental variables and species composition of minerotrophic mires have been studied mainly in spring fens in the Alps (Gerdol 1995, Bragazza & Gerdol 1999, Conradi & Friedmann 2013, Sekulová et al. 2013) and Western Carpathians (Hájek et al. 2002, Hájková & Hájek 2004, Sekulová et al. 2011, Koczur & Nicia 2013). The fens on the Bohemian Massif are little studied despite the fact that they are an important but deteriorating hotspot of central-European fen biodiversity. The regions in the Bohemian-Moravian Highlands and Třeboň basin are especially important for conservation of central-European fen biodiversity. This landscape is exceptional within the Czech Republic in the occurrence of minerotrophic mires (Divíšek et al. 2014) and especially in the occurrence of rich fens with calcium-tolerant peat mosses of the *Sphagno warnstorfii-Tomentypnion* alliance (Rybníček et al. 1984, Hájek & Hájková 2011). The latter type of vegetation, despite having been seriously affected by human activities since the 1970s (e.g. Růžička 1989), still harbours highly endangered vascular plants such as *Carex limosa*, *C. dioica*, *C. chordorrhiza* and *Trichophorum alpinum* (Růžička 1999, Navrátilová & Navrátil 2005), bryophytes such as *Meesia triquetra*, *Paludella squarrosa* and *Hamatocaulis vernicosus* (Štechová et al., in prep.) and invertebrates such as the glacial relict snails *Vertigo geyeri* and *V. liljeborgii* that are extremely rare in temperate Europe (Schenková & Horsák 2013, Schenková et al. 2013). Currently there is only data on the vegetation-environmental relationships for the Třeboň basin (Navrátilová et al. 2006) and for only small regions of the Bohemian-Moravian Highlands (Rybníček 1974, Štechová et al. 2012, Peterka 2013). Therefore there is need for a study that covers the entire hotspot area and directly analyses the relationships between water chemistry and vegetation diversity.

The specific question that should be addressed by such a study on the Bohemian Massif is the floristic and environmental delimitation of the *Sphagno warnstorfii-Tomentypnion* fens. This vegetation alliance is well known among Czech vegetation scientists and nature conservationists because it includes a large number of red-listed plants and animals. Surprisingly, the *Sphagno warnstorfii-Tomentypnion* alliance is not currently recognized in neighbouring Germany (Pott 1992, Berg et al. 2004), Poland (Matuszkiewicz 1982) and even Austria, which shares the eastern part of the Bohemian Massif with the Czech Republic (Steiner 1993, Zechmeister & Steiner 1995). Analogous vegetation types are recognized in these countries only at a very fine (subassociation) level (Steiner 1992). The reason is in these countries different classification criteria are used to delimit alliances and associations. In Germany and Austria authors predominantly use a syntaxonomical system based on floristic differentiation by dominance of vascular plants specialized to fens but having a wide pH-niche. This system was introduced by Oberdorfer (1957, 1998) and Dierssen (1982) and accepted in many other vegetation surveys across Europe (e.g. Steiner 1992, Coldea et al. 1997, Lájer 1998, Jermacāne & Laiviņš 2001). In this system, the major division is between topogenic, extremely waterlogged fens (*Caricion lasiocarpae*, *Rhynchosporion albae*) and spring fens plus fen grasslands (*Caricion davallianae*, *Caricion fuscae*). An alternative classification at the alliance level reflects the “poor-rich” gradient as the main compositional change within fens and in particular emphasising the role of bryophytes. This concept was introduced by Fennoscandian botanists (du Rietz 1949, Dahl 1956, Persson 1961, Eurola 1962, Moen et al. 2012) and was adopted among others in the former Czechoslovakia (Rybníček et al. 1984) and thereafter in Czech and Slovak republics (Dítě et al. 2007, Hájek & Hájková 2011). The *Sphagno warnstorfii-Tomentypnion* fens are a separate unit in this system. Some syntaxonomical systems are transitional but the *Sphagno warnstorfii-Tomentypnion* alliance or an analogous alliance is distinguished in some regions of Bulgaria (Hájek et al. 2008), France (Gillet 1982), Scotland (Prentice & Prentice 1975), Russia (Koroleva 2001, 2006, Lapshina 2010), Greenland (Molenaar 1976) and partially in Italy (Gerdol & Tomaselli 1997) and Ukraine (Felbaba-Klushina 2010). Hájek et al. (2006) have demonstrated that in the Western Carpathians and Balkans the four vegetation types delimited along the poor-rich gradient (*Caricion davallianae*, *Sphagno warnstorfii-Tomentypnion nitentis*, *Caricion fuscae* [=*Caricion canescenti-nigrae*], *Sphagno-Caricion canescentis*) are well separated in terms of water pH and total mineral richness, i.e. the factors that shape the major gradient in vegetation. However, one may argue that this pattern may not be so simple in regions with different water chemistry, or in regions where topogenic fens are common. The challenge is therefore to test directly the floristic delimitation of the major alliances distinguished along a poor-rich gradient using numerical classification on the Bohemian Massif.

The main aims of this study are summarized as follows: (i) to reveal major gradients in species composition of vascular plants and bryophytes in fens in the eastern part of the Bohemian Massif and their relationships to water chemistry, pH and water table depth, (ii) to test the validity of delimiting the main vegetation alliances as parts of a poor-rich gradient, including the *Sphagno warnstorfii-Tomentypnion* alliance, on the Bohemian Massif, (iii) to test the differences in environmental factors among these alliances.

Material and methods

Study area

The Bohemian Massif is a large crystalline massif located in the central part of the Czech Republic, eastern Germany, southern Poland and northern Austria. The study area (Fig. 1) is in the south-eastern part, namely the Bohemian-Moravian Highlands and Třeboň basin, where there is a great diversity and wide distribution of fens (Hájek & Hájková 2011). Two localities were sampled on the East Bohemian cretaceous table close to the boundary with the Bohemian-Moravian Highlands.

The geological substrate of the Bohemian-Moravian Highlands consists mostly of crystalline rocks of proterozoic and paleozoic age, i.e. of different kinds of gneiss, migmatite, granite, granodiorite or phyllite with small bodies of amphibolites, marbles, serpentinites or erlans. Calcium-rich cretaceous sandstone and claystone occur locally in the "Dlouhé meze" area. The Bohemian-Moravian Highlands are in the cold-temperate climatic region with a mean annual temperature of 5.0–6.5 °C and mean annual precipitation of 600–900 mm (Čech et al. 2002). The altitude at the localities studied ranged between 450 and 730 m a.s.l.

The geological bedrock in the Třeboň basin is made up of siliceous cretaceous and tertiary sandstones. The climate is temperate with a mean annual temperature of 7.8 °C and mean annual precipitation of 600–700 mm (Albrecht et al. 2003). All the study sites are located at altitudes of between 410–480 m a.s.l.

Vegetation data sampling

We sampled all the well-preserved fens with rare species in the study area. We omitted only those fens with abundance of grassland species, which are usually drained or eutrophicated; they mostly belong to the *Calthion* alliance. Further, we omitted some depauperate poor fens that lacked rare species in order to balance the data set, because poor fens prevail over rich and extremely rich fens in the current Bohemian Massif landscape. Usually a single phytosociological relevé was gathered per fen (in central, visually the most preserved part), but in some cases, two plots of two distinct types of vegetation (according to Hájek et al. 2006) were sampled at one large well-preserved locality. Both vascular plants and bryophytes were recorded within each plot (16 m^2). Their cover was estimated using the nine grade Braun-Blanquet's scale (van der Maarel 1979). Altogether the vegetation at 57 plots (see Table 1) was recorded. Bryophytes were collected from the plots and their identification was confirmed or revised using light microscope. Coordinates of relevés were obtained

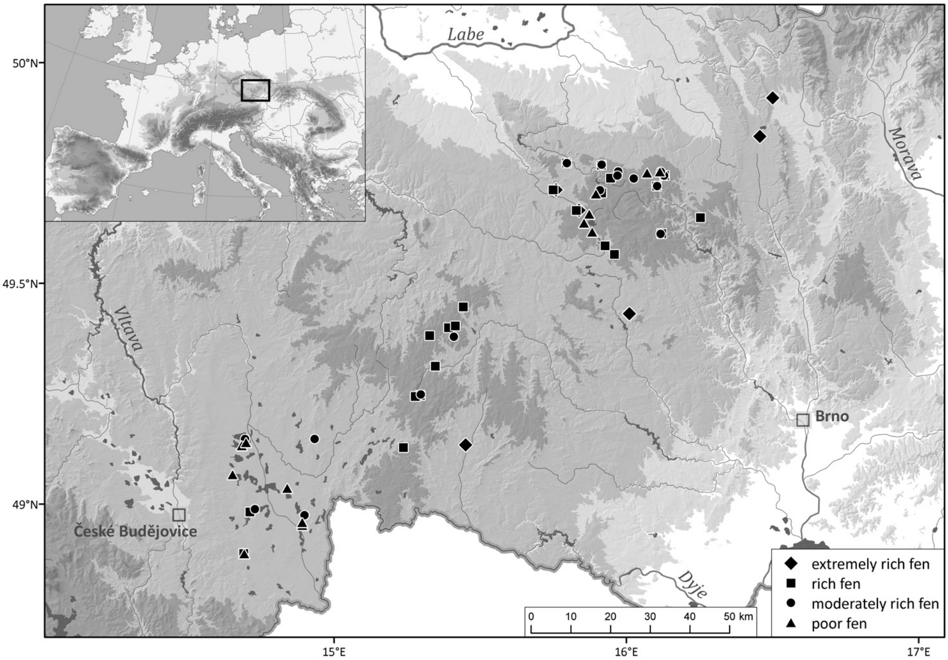


Fig. 1. – Map of plots studied on the Bohemian Massif. Their classification as particular types of fens follows the results presented in Table 1.

using the WGS84 system. Nomenclature of vascular plants follows Danihelka et al. (2012). Nomenclature of bryophytes follows Kučera et al. (2012), but the species *Plagiomnium affine*, *P. elatum*, *P. ellipticum* and *P. medium* were merged into the *Plagiomnium affine* aggregate, because of their similar indication values within fens and identification uncertainities in the case of some specimens. By analogy, *Chiloscyphus polyanthos* and *C. pallescens* as well as *Campylium stellatum* and *C. protensum* were merged. For author references of syntaxa see Hájek & Hájková (2011).

Sampling of environmental data

In summer 2011, the following environmental factors were recorded in each vegetation plot in the field using shallow bore holes dug in the peat: pH, corrected conductivity and water table depth (WTD). Samples of groundwater and biomass of (1) 2–3 (4) dominant species of moss were also collected (for details see Electronic Appendices 1, 2). Water pH and conductivity, both standardized at 20 °C, were measured in situ using portable instruments (GMH 3410 and GMH 3530 Greisinger). Conductivity due to H^+ was subtracted (Sjörs 1952). Water table depth was expressed as the mean distance between the surface of the moss cushion (i.e. the apical part of acrocarpous and pleurocarpous mosses or capitula of *Sphagna*) and actual water level. Water samples were also collected from shallow bore holes, water was pumped out of them, which were then allowed to refill before sampling. Water samples were immediately filtered through microfibre glass filters, Fisher F261, with pores of 1.2 μm and placed in plastic bottles. Preservatives were added to two separate samples: for metallic elements (0.5 ml of 65% HNO_3 per 100 ml of sample) and for anions

(0.3 ml of chloroform per 100 ml). The bottles were kept and transported to the laboratory in a portable fridge. For the analysis of N:P ratios in the biomass of moss, capitulas of sphagna and apical segments of other species of moss (length of about 2 cm) were collected using clean stainless-steel tweezers. All biomass samples were put in paper bags and left to dry out.

Water and biomass analyses

Water samples were analyzed for concentrations of NH_4^+, NO_3^-, PO_4^{3-}, K^+, Ca^{2+}, Mg^{2+} and Fe. Ammonium, nitrates and phosphates were analyzed using flow injection analysis (FIA). Other elements were determined using an atomic absorption spectrometer (AAS) novAA ® 350 (Analytik Jena AG). Flame method was used for all the above mentioned elements and ions. Lanthanum chloride was used as an ionization suppressant for calcium and magnesium analyses, and cesium chloride was used as the deionization agent when determining potassium.

Concentrations of nitrogen and phosphorus in bryophyte biomass were determined using FIA after the dried moss shoots were digested in acid (perchloric acid for determining total phosphorus and Kjeldahl digestion with sulphuric acid for ammonium).

Data processing

The phytosociological relevés were exported into JUICE 7.0 software (Tichý 2002). In order to test the applicability of the classification system based on four vegetation types (alliances) of fens, defined as part of the pH/calcium gradient (Hájek et al. 2006, Hájek & Hájková 2011), we used an unsupervised non-hierarchical numerical classification algorithm ISOPAM (Schmidtlein et al. 2010) at the level of four clusters. The ISOPAM algorithm is based on the classification of ordination scores from isometric feature mapping. Ordination and classification are repeated in a search for groups rich in diagnostic species and high overall fidelities of species to particular clusters. This approach is beneficial when the data sets have a bad "signal to noise ratio" (Schmidtlein et al. 2010) such as those for small fens and fen grasslands where a few fen specialists are accompanied by a high number of more ubiquitous wetland and grassland species coming from the surroundings. In the ISOPAM algorithm, we applied default threshold for diagnostic species filtering and the Bray-Curtis distance to ordinate the relevés. The ISOPAM algorithm considers only the presence-absence data. We identified three spuriously classified relevés (no. 2, 26 and 55 in Table 1) whose dominant species and/or overall species composition deviated from the characterization of this vegetation type (alliance) in the Vegetation of the Czech Republic monograph (Hájek & Hájková 2011). We checked their assignment to the resulting clusters using the normalized weirdness method (van Tongeren et al. 2008), which indicates they be placed in a more appropriate group. The diagnostic species of a particular cluster were determined using the phi-coefficient (Chytrý et al. 2002) with the size of all the groups standardized to the same size. For table presentation (Table 1) the species with fidelity to a particular type of vegetation with a phi > 0.3 were regarded as diagnostic. The significance of fidelity was verified using Fisher's exact tests ($P < 0.05$). Three grassland generalist that appeared to be diagnostic for a small group of extremely-rich fens (*Agrostis capillaris*, *Cirsium rivulare*, *Vicia cracca*), although they occurred in only two relevés with low abundance, were reclassified as accompanying species.

Main gradients in the floristic composition of relevés were assessed using detrended correspondence analysis (DCA). The vegetation data were further subjected to canonical correspondence analysis (CCA) to find the best significant predictors of species composition using a forward selection procedure and the Monte Carlo permutation test (499 permutations) with Holm correction of P values (referred to as P_{adjust}). Three vegetation matrices, with transformed cover values (arcsin transformation) and down weighting of rare species were subjected to correspondence analyses (both DCA and CCA): (i) both vascular plants and bryophytes, (ii) only vascular plants and (iii) only bryophytes. With the exception of pH, no environmental variables had normal or uniform distributions (Shapiro-Wilk test). Therefore, their values were logarithmically transformed to approximate a normal distribution. The two major gradients were ecologically interpreted by a posteriori plotting the isolines of measured environmental factors using generalized additive models (GAMs) with Poisson distribution and stepwise selection of complexity using Akaike information criteria. Species richness of vascular plants and bryophytes were also modelled in order to illustrate changes in diversity of both taxonomic groups along the main floristic gradients.

Principal component analysis (PCA) was used to describe the relationships between particular environmental variables, and check whether the group of measured environmental factors as a whole describes sufficiently the floristic differences between the different vegetation types. We applied PCA to the environmental data matrix, with centering by particular environmental variables, and plotted the delimited types of vegetation *a posteriori* onto the resulting plot. The CANOCO 5 package (Šmilauer & Lepš 2014) was used for the ordination analyses and GAM modelling. The N:P ratio in moss biomass was not included in the multidimensional analyses because of lack of statistical independence; moss element concentrations depend not only on the environment but also on species identity (Hájek et al. 2014) and their effects may therefore be overestimated when environmental factors are confronted with the results of PCA or DCA.

Significance of differences in measured environmental factors among the different vegetation types was tested using one-way ANOVA in the STATISTICA software (version 12, StatSoft Inc.) and the unequal N HSD post-hoc test. As conductivity, magnesium content and water table depth did not meet the assumptions required for parametric ANOVA (homoscedasticity in most cases) even after the logarithmic transformation, nonparamatric Kruskal-Wallis statistics were used in these cases. We further compared the major vegetation types in terms of the N:P ratio in bryophyte samples to determine whether the observed differences in P concentration in water coincide with the N:P ratio, which may indicate P-limitation of aboveground production.

Results

Classification of vegetation

The ISOPAM algorithm at the level of four clusters gives a result that is similar to the expert-based classification presented in the Vegetation of the Czech Republic with the exception of only three relevés. In combination with the matching produced by the normalized wierdness method the end result was in complete agreement with the expert-based national vegetation classification. In particular four major vegetation types (Table 1) could be characterized as follows:

Table 1. – Phytosociological table of individual relevés with Braun-Blanquet cover codes (a = 2a; b = 2b). Diagnostic species of particular vegetation types (in bold) are sorted according to fidelity, other species are sorted according to frequency. Codes in second column refer to red lists status of species (according to Grulich 2012, Kučera et al. 2012), except for category LC of bryophytes. Shortened names of localities and geographical coordinates are listed below the table. For the full header data see Electronic Appendix 1.

Relevé Nr.			1111111111222222222	2333333333344444	4444455555555
		123456	7890123456789012345678	9012345678901234	5678901234567
Caricion davallianae					
Triglochin palustris	C2	**+**+.b.+	..........+...........	....	....
Palustriella commutata		**a**+...+	....	....	....
Phragmites australis		**1**.a.ra	...a...+a..a........1.	....	...+1........
Blysmus compressus	C2	**.**.1a..	....	....	....
Eupatorium cannabinum		**+**...1.	....	....	....
Carex davalliana	C2	**1**...a1	.........b....ab..a.a.	....	....
Carex paniculata	C4a	**.**...a+	....................+.	....	....
Fissidens adianthoides	LC-att	**+**+...+	++......+...1.+....+..	....	....
Scorpidium cossonii	LR-nt	**5**5...b	........b31...++....+.	....	....
Sphagno warnstorfii-Tomentypnion					
Sphagnum warnstorfii	LC-att	......	**a**.53a1a.1++b+4414aa443	..a.............	....
Anthoxanthum odoratum		......	**+**+11+1+++.11+.+a+11++.	...1.......+.1.+	....
Luzula multiflora		......	**+**++1++.++.++..+++++.r+	..+......+...+..	...........+.
Sphagnum contortum	LR-nt	......	**3**..b+1..a1b.+1+.1+.+.4	....4.+.........	....
Festuca filiformis		......	**.**+..+++.+.....++..a+.+	....	....
Sphagnum teres		......	**1**41335a3..33+b1+a11+11	1...+a.+33..34b.	....+........
Trichophorum alpinum	C2	......	**+**.....r1+1+...+....+.+	....	....
Carex pulicaris	C2	......	**.**..1....++.1..11..+1..	....	....
Briza media		...+.r	**+**+1+.+1.+.11+1++..+11.	...+.........+..	....
Plagiomnium affine agg.		++.+1+	**1**1+++++++++13+++.++1++	............+++.	....
Valeriana dioica	C4a	++.1.a	**1**1+1+++++++1111abba1b+	.....+.r11+.1a1.	....
Holcus lanatus		...+..	**+**.1.++++r+1a+++1.r..+.	..11........11..	....+........
Tephroseris crispa	C4a	......	**.**..+.+++..++.....+r+..	..........r.....	....
Galium uliginosum		...+++	**+**++++++++.++++++++++++	..++...++++.++++	....
Cirsium palustre		..1+..	**+**++++.++++1+1++++11+.+	r.1+...+++.+++++	....
Bryum pseudotriquetrum		11b1.+	**+**++++++.++.+1+++.+++++	.........+......	....
Carex echinata		......	**+**.1++1.111+11.+1+a++.+	..11...b++.a+a.+	.....+...+.a.
Paludella squarrosa	EN	......	**.**......r..+..+..+..+1.	....	....
Breidleria pratensis	LC-att	......	**.**..1+...+...++++1.1+..	..1.........1+..	....
Dactylorhiza majalis	C3	.+...+	**+**++..+.+..1+.+.++.+.++	............+...	....
Potentilla erecta		++..+b	**+**11+1111++11+1+1++111+	..1+....++.+1+++	....+...++.+.
Carex panicea		b1.11a	**3**aa1111a+b1+ba33baa333	...+.1.+.a.+a3ba	....a......+.
Philonotis fontana		......	**+**...+...1.......++....	....	....
Calliergonella cuspidata		+..1a1	**1**.11a1++3+1+31+b14aa++	..+.11++31b.b+b.	....+........
Carex demissa		...+..	**+**...+..1++..+.+++1...+	..1.....+....+..	....
Aulacomnium palustre		...+.+	**.**b1+111.+.b+++a++1b11+	...++++.ab+..++.	.+..+....+.+.
Crepis paludosa		+....+	**1**1...1...+.1.++a111+a+	...........aa+++	....
Festuca rubra agg.		..1+r.	**+**+++++1+..+1+1+1+.++1r	+++....+++.++1++	...........+.
Equisetum fluviatile		......	**.**+1.++.1..++1+.++r.+..	+.+.+.++.r++....	....+........
Carex flava	C4a	......	**.**++.++................	....	....
Sphagnum subnitens	LC-att	......	**.**.......1.......+.+.+.	....	....
Menyanthes trifoliata	C3	.b...a	**.**++13.++..+aa3.+...b.1	...+aa.4........	....
Ranunculus acris		....+.	**r**+++.+.....++++.......	...........r.+..	....
Chiloscyphus pallescens/polyanthos		......	**.**.........+....++.+r..	..+.............	....
Myosotis nemorosa		......	**.**....+....+.....+r+...	.........r......	....
Succisa pratensis		.+....	**.**...+.+.+..++.+1...+a+	..++...+.+......	....
Climacium dendroides		...+.+	**a**1...+..+..1++.++.a+..	..........+.1+..	....

Relevé Nr.		 123456	1111111111222222222 7890123456789012345678	2333333333344444 9012345678901234	4444455555555 5678901234567
Caricion canescenti-nigrae					
Carex canescens		......	....++.++.............	**b**11.1.+1+1++.1++	.........+.++
Galium palustre agg.		..1+..	..++++...++.++...+...+	**+**+++.+++r+1.++++	....
Veronica scutellata	C4a	......	....	........++r.++..	....
Agrostis canina		......	+.++++++..++1+++++++++	**1**111++111+++1b1+	...+++.++..a+
Comarum palustre	C4a	......	..b+aa11..ba.+.......+	.baa3aa.+33...4.	...a.........
Straminergon stramineum		......	..+++++++.+..+.++1++.+	**+**+++++11++..++++	..+.+...+++++
Bistorta officinalis		......	.....r......+.........	........++.11.+.	....
Carex nigra		.+++..	++1+1ba.1.a1a1..1+.+.+	**b**1b+++11+31+51a1	.+++++..+1++.
Ranunculus flammula		......	.....+...........+....	........++..+1..	....
Sphagno-Caricion canescentis					
Polytrichum commune		......	.....+................	.1....+.........	**+**+++.1+.+baa+
Sphagnum fallax		......	.....1..++a..++.......	5......3.....+.1	**5**43ba51154515
Vaccinium oxycoccos	C3	......	.......1.11...........	....	**1**a.1aa1...1..
Pinus sylvestris juv.		..+...	........++............	.....+1.........	**+**+++++++.....
Sphagnum papillosum		......	.........+............	....	.3b.4...1....
Rhynchospora alba	C2	......	.........r............	....	..+.1.1+.....
Drosera rotundifolia	C3	...+..	....+.+++1+...+.+.+r+1	.....1+.........	**+**+111++++....
Calluna vulgaris		......	......+...............	....	**+**+..+........
Picea abies juv.		......	..................+...	....	.+.......++..
Utricularia ochroleuca	C1	......	....	.....+..........	...+..++.....
Avenella flexuosa		......	....	....	.........a.+.
Sphagnum capillifolium		......	....	....	.1..1........
Caricion davallianae and ***Sphagno warnstorfii-Tomentypnion***					
Tomentypnum nitens	LR-nt	**+**114.4	.a+1.+.+...1.1b41+abb.	....	....
Campylium stellatum	LR-nt	**1**1+a+b	+1.+++1+131++1+.+.+1+1	..+.+.+.+.......	....
Sphagno warnstorfii-Tomentypnion and ***Caricion canescentis-nigrae***					
Viola palustris		......	**+**.+++1+1+++++++.1a++++	1+1+.+1a+111++++	...++...rr.1.
Other species					
Eriophorum angustifolium		+.+1..	++aa+111++1+a1+14+ab+b	1a1++1+113.1+b3a	ba+1+11b1.++.
Lysimachia vulgaris		..1++.	....+.++++++.+++++..++	.r+.1+1+r++1.+++	...++..+...+.
Carex rostrata		++a14.	...++.b.+.+1a+.+...+.+	...+11+++++.....	..a+a..+....3
Epilobium palustre	C4a	..a++r	..+..++.++.++..r+..r.r	..+++..+r++r++++	...+..r......
Molinia caerulea agg.		1+a..+	.a...+...1+...3+...a1.	...1+a...a+.....	.+a.a11+a.1..
Sphagnum palustre		......	....+.b.+.1a..1...a+.+	.++411+..+...1.3	...4.+51.1.1.
Rumex acetosa		..a+..	+.+..+++..+++..++.+...	.......+r+.++++.	...........r.
Sphagnum flexuosum		......	...........a...+a1..1+	a.1b.a.....5.b14	..ba1.1....5.
Cardamine pratensis		..++..	..+.+++...++.+...+++.+	+.......+++.+...	....
Equisetum palustre		+1...+	.+1........1..++..+++.	+......+.++.b+..	....
Juncus articulatus		...+++	....++.+.+1.+1+++....+	.....+.......+..	....+........
Juncus effusus		......	........+++....++r....	...+...+...+++++	.....++..+.+.
Lychnis flos-cuculi		..+.+.	+.++.+....+..+..r.r..+	.........r..+++.	....
Aneura pinguis		.+.+..	.+..+..+++....+.+....+	..+..++.........	....
Angelica sylvestris		....+.	..+...+.+.++...rr..+..	..+.....+.....1.	....
Alnus glutinosa juv.		.....+	....r1...+.....+.+..++	.....1..+..+.+..	....
Sanguisorba officinalis		......	+1.............1++.+..	...........a1++.	...........1.
Juncus bulbosus		......	+....+..........r1+..+	.....+.......+..	...++..1.....
Filipendula ulmaria		....+r	.+.........a.+.r...+.r	..a.......+.....	....
Mentha arvensis		....+.	+....++...+..+...+....	........++....1.	....
Ranunculus auricomus agg.		......	..+..........+.+.r+...	........++..+++.	....
Peucedanum palustre		......	..........+..+.....+..	...++++.1.......	...+...+.....

Relevé Nr.		123456	1111111111222222222 7890123456789012345678	2333333333344444 9012345678901234	4444455555555 5678901234567
Hamatocaulis vernicosus	VU	.1.+..	.+.+.........+...+.+.+	..........+.....	....
Parnassia palustris	C2	.+.1..	.+.+....+.+.++......+.	....	....
Salix aurita juv.		...+..	...++...+........r...+	..+..++.........	....
Juncus conglomeratus		......	..+..+....r.+.+...r...	............+++.	....
Polytrichum strictum		......	..r.+.1............+..	...+............	.1.++...+....
Betula pendula juv.		......	...+..............+.++	.....+1.........	....+....+.+.
Caltha palustris		......	.....+....r++.........	+......+.+..+.r.	....
Equisetum arvense		...+r.	1....++........+r.+...	....	....
Frangula alnus juv.		.....+	......+...+.......+.+.	.....+..........	...++........
Sarmentypnum exannulatum		......	....1+...............+	+...11+.........	...+.........
Eriophorum latifolium	C2	++....	1b......1.....+.....+.	....	....
Carex diandra	C2	...a..	....b..+.....1.......+	.....1....b.....	....
Cirriphyllum piliferum		....++	...............++.+...	.........+..+...	....
Nardus stricta		......	..+..............++...	...+.........+.+	........+....
Sphagnum subsecundum		......	.......11.............	..1..3b...a.....	....a........
Carex lasiocarpa	C3	......	.......+.+............	......1.4.1.....	...+..1......
Equisetum sylvaticum		......	.........+....+.+.....	...........r+...	.........+.+.
Linum catharticum		.+....	.+.......+..+.r......+	....	....
Lycopus europaeus		...++.	....r........+........	..+.............	.......r.....
Scutellaria galericulata		....+.	.............+........	.......++++.....	....
Lysimachia thyrsiflora	C3	......	.....r...++...........	...++.1.........	....
Rhytidiadelphus squarrosus		......	............+..+..1...	............++..	...........+.
Calliergon giganteum	VU	.+.+..	....+..............+.1	....	....
Carex dioica	C1	......	.1....+......+.....+..	....	....+........
Anemone nemorosa		......	..............+++.1...	............+...	....
Epipactis palustris	C2	+....a	...............1....a.	....	....
Scirpus sylvaticus		...+a.	....	.......+........	.........+...
Lythrum salicaria		...+..	.........r............	....	...++........
Salix pentandra juv.	C4a	....+.	.+.+...+..............	....	....
Salix cinerea juv.		......	.+.....+..............	......a.........	....+........
Quercus petraea juv.		......	........+.............	...+............	.+...+.......
Juncus filiformis		......	.............+........	.......+.+....+.	....
Sphagnum inundatum		......	.................+...+	.............+..	...1.........
Carex lepidocarpa	C2	.a....	........1...........r.	....	....
Cirsium rivulare		....++	............+.........	....	....
Ranunculus repens		....+.	+................r....	....	....
Vicia cracca		....r+	.+....................	....	....
Dicranum bonjeanii	LR-nt	......	.+......+.............	..+.............	....
Leontodon hispidus		......	......+.......a...1...	....	....
Carex chordorrhiza	C1	......	.......1..............	....a...........	..........+..
Juncus bufonius agg.		......	........+++...........	....	....
Brachythecium mildeanum		......	...........+1+........	....	....
Prunella vulgaris		......	.............1+..+....	....	....
Calliergon cordifolium		......	................+.....	..........4.+...	....
Utricularia intermedia	C1	......	....	....1.1.........	...1.........
Agrostis capillaris		..1.+.	....	....	....
Poa trivialis		..1...	.........+............	....	....
Polygala amarella	C4b	.....+	.+....................	....	....
Selinum carvifolia		......	.1...................+	....	....
Lathyrus pratensis		......	.++...................	....	....
Geum rivale		......	.+.........1..........	....	....
Carex flacca		......	.+................a...	....	....
Sphagnum angustifolium	LC-att	......	......1...............	.5..............	....
Betula pubescens juv.		......	.......1..............	....	....+........
Sphagnum auriculatum		......	.......1..............	....	.......5.....

Relevé Nr.			1111111111222222222	2333333333344444	4444455555555
		123456	7890123456789012345678	9012345678901234	5678901234567
Carex limosa	C2	......	.......r..............	....	...a.........
Riccardia multifida	LC-att	......	........+.+...........	....	....
Drosera anglica	C1	......	........+.............	....	....+........
Pleurozium schreberi		......	..........+.......+...	....	....
Luzula sudetica	C3	......	............+......r..	....	....
Achillea millefolium agg.		......	............+.........	............r...	....
Danthonia decumbens		......	..............+...+...	....	....
Carex hostiana	C2	......	..............+.....+.	....	....
Carex hartmanii	C4a	......	...............1......	..............+.	....
Chiloscyphus cuspidatus		......	................+.....	....	...........+.
Sorbus aucuparia juv.		......	.................rr...	....	....
Vaccinium myrtillus		......	..................+...	....	....+........
Hypericum maculatum		......	..................r...	.............+..	....
Sphagnum fimbriatum		......	....	..4...4.........	....
Brachythecium rivulare		......	....	..1...........+.	....
Deschampsia cespitosa		......	....	..+.............	...........+.
Sphagnum russowii		......	....	...1............	.........+...
Carex elongata		......	....	.....+..........	....1........
Carex elata	C2	......	....	......1.........	......+......
Holcus mollis		......	....	.......+........	...........+.
Calamagrostis villosa		......	....	...............a	.........3...
Trientalis europaea	C4a	......	....	...............+	.........a...
Eriophorum vaginatum		......	....	...............+	..........1..

Species recorded within one relevé. Vascular plants: *Gymnadenia densiflora* (C1) 1: +; *Eleocharis quinqueflora* (C1) 2: a; *Utricularia minor* (C2) 2: +; *Typha angustifolia* 4: r; *Galium mollugo* agg. 5: +; *Poa pratensis* 5: +; *Aegopodium podagraria* 5: +; *Calamagrostis epigejos* 5: +; *Acer pseudoplatanus* juv. 7: +; *Carex appropinquata* (C3) 8: a*;* *Lotus corniculatus* 8: +; *Dactylorhiza fuchsii* (C4a) 10: +; *Laserpitium prutenicum* (C3) 13: +; *Juncus alpinoarticulatus* (C3) 15: +; *Drosera intermedia* (C1) 15: +; *Pinguicula vulgaris* (C2) 15: +; *Drosera ×obovata* 15: +; *Quercus robur* juv. 16: +; *Poa palustris* 18: +; *Cirsium heterophyllum* 19: +; *Equisetum ×litorale* 19: +; *Persicaria maculosa* 20: +; *Scorzonera humilis* (C4a) 22: b; *Carex pilulifera* 22: +; *Alchemilla* sp. 22: +; *Listera ovata* (C4a) 25: +; *Primula elatior* 25: +; *Ajuga reptans* 25: +; *Maianthemum bifolium* 25: +; *Salix euxina* juv. 28: r*;* *Carex vesicaria* 31: +; *Calamagrostis canescens* 33: 1; *Crepis mollis* subsp. *succisifolia* (C3) 37: +; *Pedicularis palustris* (C1) 39: +; *Eleocharis mamillata* (C4a) 39: +; *Lotus pedunculatus* 41: 1; *Pedicularis sylvatica* (C2) 42: +; *Fraxinus excelsior* juv. 42: +; *Dryopteris* sp. 43: +; *Sparganium natans* (C2) 48: 1; *Typha latifolia* 48: +; *Nymphaea candida* (C1) 48: +; *Vaccinium vitis-idaea* 49: +; *Eriophorum gracile* (C1) 49: +; *Galium saxatile* 54: +; *Senecio nemorensis* agg. 54: +; *Andromeda polifolia* (C2) 55: 1; *Melampyrum pratense* 55: +. Bryophytes: *Philonotis calcarea* (LC-att) 2: 1; *Cratoneuron filicinum* 3: 4; *Atrichum undulatum* 7: +; *Calliergonella lindbergii* 7: +; *Sphagnum centrale* (LC-att) 9: 1; *Sphagnum magellanicum* 13: 3; *Sphagnum obtusum* (LR-nt) 14: 4; *Calypogeia azurea* 15: +; *Pseudocampylium radicale* (LC-att) 31: +; *Polytrichum longisetum* 31: +; *Brachythecium rutabulum* 31: r; *Amblystegium serpens* 33: +; *Dichodontium palustre* (LC-att) 34: +; *Pohlia nutans* 34: +; *Pohlia drummondii* 49: +; *Plagiothecium denticulatum* 54: +.

Localities of relevés (BHM = Bohemian-Moravian Highlands, TR = Třeboň basin): **1**. Eastern Bohemia, Opatov, 0.5 km S of the Nový rybník pond, 49°49'39.1", 16°29'18.9". **2**. BMH, Hluboká, Řeka Nature Reserve, 0.5 km NNW of the village, 49°39'59.8", 15°51'10.7". **3**. BMH, Bory-Dolní Bory, 0.3 km NW of Horník pond, 49°25'52.6", 16°01'24.6". **4**. BMH, Černíč, 1.2. km NW of village, 49°08'15.6", 15°27'09.2". **5**. Eastern Bohemia, Rudoltice v Čechách, 3.5 km NW of train station, 49°54'52.2", 16°32'10.1". **6**. BMH, Sobíňov, Zlatá louka Nature Reserve, 2 km N of village, 49°42'49.6", 15°46'23.0". **7**. BMH, Věcov-Odranec, S margin of village, 49°36'41.3", 16°08'23.1". **8**. BMH, Hluboká, Řeka Nature Reserve, 0.5 km NNW of village, 49°39'58.1", 15°51'10.7". **9**. BMH, Milíčov, N of village, 49°24'11.3", 15°23'43.1". **10**. BMH, Dušejov 1 km W of village, 49°24'26.2", 15°25'09.1". **11**. BMH, Šimanov, S of village, 49°27'00.6", 15°26'49.3". **12**. BMH, Nový Rychnov-Čejkov, 1 km N of village, 49°23'06.8", 15°19'46.5". **13**. BMH, Švábov, 0.5 km WNW of train station, 49°18'58.8", 15°20'55.1". **14**. BMH, Jihlávka, 1 km S of village, 49°15'00.7", 15°17'48.6". **15**. TR, Borovany-Hluboká u Borovan, 1,5 km SE of the village, 48°53'30.6", 14°41'16.5". **16**. TR, Libín-Spolí, in the valley of the Spolský potok stream, N of village, 48°59'09.6", 14°42'32.1". **17**. TR, Kunžak-Suchdol, N of village, 49°07'54.7", 15°14'14.4". **18**. BMH, Jihlávka, 1,2 km SE of village, 49°14'51.6", 15°16'44.4". **19**. BMH, Žďár nad Sázavou-Plíčky, 49°33'57.2", 15°58'27.6". **20**. BMH, Žďár nad Sázavou, N of town, 49°35'07.8", 15°56'32.4". **21**. BMH, Trhová Kamenice, Buchtovka Nature Reserve, S of village, 49°46'26.6", 15°48'38.9". **22**. BMH, Hlinsko, Ratajské rybníky Nature Reserve, SE of town, 49°46'06.1", 15°55'58.3". **23**. BMH, Pustá Rybná, Damašek Nature Reserve, 1.5 NW of village, 49°43'08.8", 16°07'29.7". **24**. BMH, Borová, 0.5 km W of train station, 49°44'34.3", 16°09'10.0". **25**. BMH, Korouhev, 1.5 km SE of village, 49°38'45.7", 16°16'31.4". **26**. BMH, Kameničky, Louky v Jeníkově Nature Reserve, 49°44'19.0", 15°57'51.0". **27**. BMH, Sobíňov, Zlatá louka Nature Reserve, 2 km N of village, 49°42'48.4", 15°46'21.2". **28**. BMH, Vortová, Zlámanec Nature Reserve, 49°42'18.9", 15°55'55.7". **29**. BMH, Věcov-Odranec, 1 km S of village, 49°36'37.6", 16°08'12.1". **30**. BHM, Hojkov, 1 km S of village, 49°22'56.8", 15°24'50.6". **31**. BMH, Jihlávka, 1,2 km SE of village, 49°15'06.7", 15°17'55.4". **32**. TR, Ratiboř, 1.5 km E of village, 49°09'06.0", 14°55'53.4". **33**. TR, Bošilec, 49°09'04.3", 14°41'27.9". **34**. TR, Odměny, near Svět pond, 48°59'31.3", 14°43'33.5". **35**. TR, Chlum u Třeboně 48°58'44.3", 14°53'49.4". **36**. BMH, Trhová Kamenice, Buchtovka Nature Reserve, 49°46'24.5", 15°48'44.3". **37**. BMH, Vortová, Návesník Nature Reserve, 49°42'41.9", 15°55'36.5". **38**. BMH, Kameničky, Bahna Nature Reserve, 49°45'11.3", 15°59'28.3". **39**. BMH, Hlinsko, Ratajské rybníky Nature Reserve, SE of town, 49°46'09.8", 15°56'01.4". **40**. BMH, Pustá Rybná, Damašek Nature Reserve, 1.5 NW of village, 49°43'08.6", 16°07'36.0". **41**. BMH, Borová, 2 km NW of village, 49°45'05.0", 16°08'26.0". **42**. BMH, Borová, 0.5 km W of train station, 49°44'32.8", 16°09'07.4". **43**. BMH, Kameničky-Filipov, S margin of village, 49°44'35.5", 15°59'18.5". **44**. BHM, Svratouch, 1 km NE of village, 49°44'12.7", 16°02'44.0". **45**. BMH, Radostín, Radostínské rašeliniště Nature reserve, 49°39'25.7", 15°53'18.4". **46**. TR, Borovany, SE of Žemlička pond, 48°53'27.7", 14°41'23.7". **47**. TR, Lišov-Dolní Slověnice, 2 km NW of village, 49°04'11.4", 14°38'55.7". **48**. TR, Ponědrážka, 1.5 km WNW of village, 49°08'09.1", 14°40'46.4". **49**. TR, Ponědrážka, 1 km NWN of village, 49°08'33.7", 14°41'39.3". **50**. TR, Hamr, SW of Kukla pond, 48°57'19.2", 14°53'21.0". **51**. TR, Hamr, 2 km NW of village, 48°57'43.0", 14°53'19.2". **52**. TR, Třeboň, 49°02'21.7", 14°50'12.1". **53**. BMH, Polnička, Pod Kamenným vrchem Nature Reserve, 49°36'59.4", 15°53'53.3". **54**. BMH, Borová, 2 km NW of village, 49°45'03.6", 16°08'13.4". **55**. BMH, Radostín, Dářko Nature reserve, 2 km S of village, 49°38'14.4", 15°52'10.3". **56**. BHM, Pustá Kamenice, S of village, 49°44'56.5", 16°05'31.4". **57**. BMH, Vortová, Malý Černý pond, 49°42'10.6", 15°54'44.9".

1. *Caricion davallianae* (extremely rich fens)

Absence of *Sphagnum* species and presence of low, calcium-demanding graminoids (*Blysmus compressus*, *Triglochin palustris*) differentiates this alliance from the others. The herb layer is further composed of sedges such as *C. davalliana*, *C. panicea*, *C. rostrata* and calcicole herbaceous plants (*Eupatorium cannabinum*, *Valeriana dioica*). The moss layer is usually dominated by *Tomentypnum nitens* or *Scorpidium cossonii*, accompained by *Bryum pseudotriquetrum*, *Campylium stellatum* or *Palustriella commutata*. Well-preserved stands of *Caricion davallianae* were recorded very rarely within the study area. All the sites studied occur at localities with stable water regimes and are regularly mown.

2. *Sphagno warnstorfii-Tomentypnion* (rich fens)

This community is characterized by presence, and often also strong dominance, of calcium-tolerant species of *Sphagnum* (*Sphagnum contortum*, *S. teres*, *S. warnstorfii* and, occasionally, *S. subnitens*). The moss layer is further enriched by so called “brown mosses”, i.e. non-sphagnaceous weft-forming bryophytes (*Campylium stellatum*, *Hamatocaulis vernicosus*, *Scorpidium cossonii*) and bryophytes with boreal distributions considered to be glacial relicts in central Europe (Rybníček 1966), e.g. *Paludella squarrosa*, *Tomentypnum nitens* and *Breidleria pratensis.* The herb layer is mostly made up of low sedges (*Carex demissa*, *C. nigra*, *C. panicea*, *C. pulicaris*), accompained by other

Cyperaceae (*Eriophorum angustifolium*, *E. latifolium*, *Trichophorum alpinum*). *Tomentypnum nitens* and *Sphagnum warnstorfii* often form small hummocks, on which species preferring drier (i.e. oxic) conditions can grow (*Anthoxanthum odoratum*, *Festuca filiformis*, *Luzula multiflora*). Both the bryophyte and herb layers are usually species-rich and host a large number of rare or endangered species (according to Grulich 2012, Kučera et al. 2012), e.g. *Calliergon giganteum*, *Carex dioica*, *C. hostiana*, *C. pulicaris*, *Dactylorhiza majalis*, *Drosera rotundifolia*, *Hamatocaulis vernicosus*, *Paludella squarrosa*, *Parnassia palustris* and *Trichophorum alpinum*. The vegetation is restricted to protected and annually mown fens and fen meadows.

3. *Caricion canescentis-nigrae* (= *Caricion fuscae*; moderately rich fens)

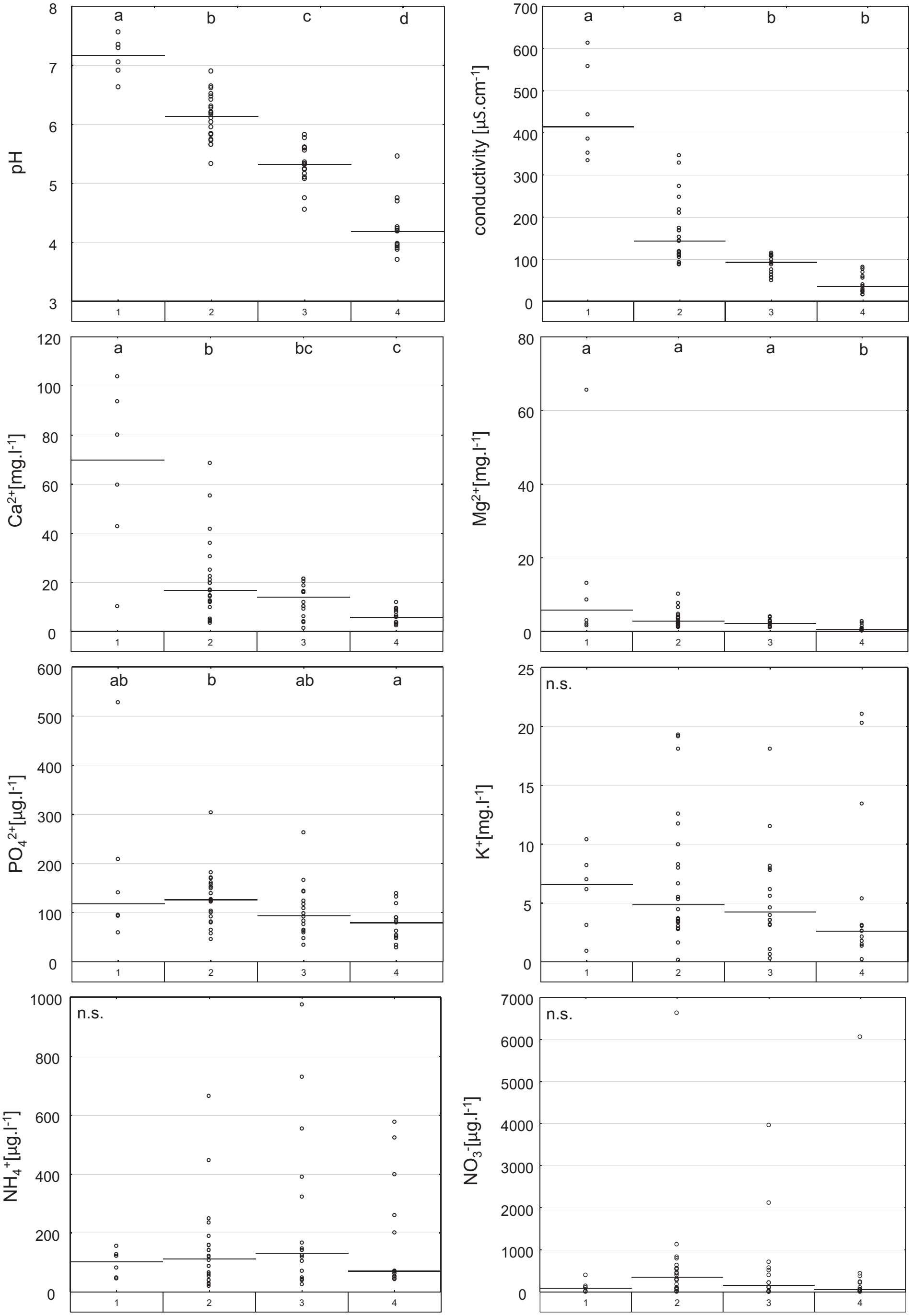
This community has a relatively low number of diagnostic species and is frequently dominated by *Carex nigra*, *Eriophorum angustifolium* and *Comarum palustre.* The moss layer comprises mostly *Sphagnum teres*, but other species of moss can also prevail (e.g. *Calliergonella cuspidata*, *Sphagnum subsecundum*). Both the herb and bryophyte layers are medium species-rich and almost lack calcicole species of plants. In some cases, the moderately rich fens in the study area lack sharp boundaries with *Calthion palustris* meadows (namely the *Angelico sylvestris-Cirsietum palustris* association) and poor fens. These transitional stands are indicated by the occurrence of broad-leaved herbaceous plants (*Angelica sylvestris*, *Bistorta officinalis*, *Caltha palustris*, *Lychnis flos-cuculi*, *Ranunculus auricomus* agg. or *Sanguisorba officinalis*) and/or an enhanced cover of *Sphagnum flexuosum.*

4. *Sphagno-Caricion canescentis* (poor fens)

This, the last alliance represents species-poor minerotrophic fens without calcium-tolerant mosses and vascular plants. Frequent dominants of the moss layer are *Sphagnum* sect. *Cuspidata* (*S. fallax*, *S. flexuosum*), *Sphagnum* sect. *Palustria* (*S. palustre*, *S. papillosum*) and *Polytrichum commune.* Other non-sphagnaceous mosses are rarely present, with the exception of *Straminergon stramineum.* The herb layer mostly consists of *Cyperaceae* (*Carex nigra*, *C. rostrata*, *Eriophorum angustifolium*) and shrubs (*Calluna vulgaris*, *Vaccinium oxycoccos*). Some mires in the Třeboň basin are characterized by a fine-scale mosaic of (i) poor fens and (ii) oligotrophic pools with rare macrophytes (e.g. *Sparganium natans*, *Utricularia ochroleuca*, *U. intermedia*) or strongly waterlogged microhabitats with *Rhynchospora alba* and *Sphagnum auriculatum*, whereas similar habitats in the Bohemian-Moravian Highlands are rather uniform. Mire vegetation of the *Sphagno recurvi-Caricion canescentis* is widespread on the Bohemian Massif and occurs in wet meadows, at the margins of fishponds, in bog laggs or treeless patches in coniferous forests.

Ecological differences between the different types of fens

The differences in the environmental variables in the four vegetation types are shown in Fig. 2. One-way ANOVA or the Kruskal-Wallis test confirmed the hypothesis that the different types of fens are well-characterized by water chemistry, especially pH, conductivity and calcium content of the groundwater. All groups differed significantly ($F = 95.61$, $P < 0.00001$) in pH, with the highest values recorded in the extremely rich fens, lower values in rich fens and moderately rich fens and the lowest values in poor fens. Similar results


pH
8
7
6
5
4
3
a
b
c
d
1
2
3
4
conductivity [µS.cm-1]
700
600
500
400
300
200
100
0
a
a
b
b
1
2
3
4
Ca2+[mg.l-1]
120
100
80
60
40
20
0
a
b
bc
c
1
2
3
4
Mg2+[mg.l-1]
80
60
40
20
0
a
a
a
b
1
2
3
4
PO42+[µg.l-1]
600
500
400
300
200
100
0
ab
b
ab
a
1
2
3
4
K+[mg.l-1]
25
20
15
10
5
0
n.s.
1
2
3
4
NH4+[µg.l-1]
1000
800
600
400
200
0
n.s.
1
2
3
4
NO3-[µg.l-1]
7000
6000
5000
4000
3000
2000
1000
0
n.s.
1
2
3
4

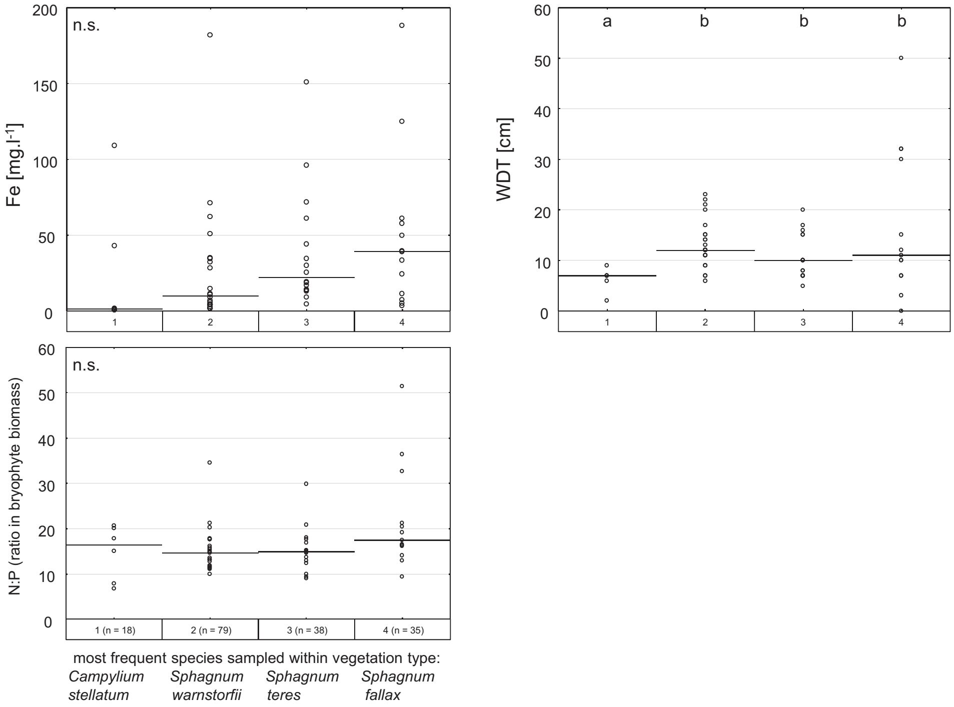


Fig. 2. – Comparison of the environmental variables and the N:P ratio in bryophyte biomass measured in the four vegetation types: 1 – *Caricion davallianae* (extremely rich fens), 2 – *Sphagno warnstorfii-Tomentypnion* (rich fens), 3 – *Caricion canescenti-nigrae* (moderately rich fens), 4 – *Sphagno-Caricion canescentis* (poor fens). Medians are indicated by horizontal lines. Significant differences between groups ($P > 0.05$, the post-hoc test) are indicated by different letters, n.s. = no significant differences.

were also recorded for conductivity ($F = 58.30$, $P < 0.00001$), calcium ($F = 14.02$, $P < 0.00001$) and magnesium (KW-H = 24.05, $P = 0.00002$), but these chemical variables did not differ between all pairs of vegetation types. Water in rich fens contained significantly more phosphorus ($F = 10.74$, $P = 0.0132$) than that in poor fens. In contrast, no significant differences were detected in the N:P ratio in the bryophyte biomass. By analogy, concentrations of NH_4^+, NO_3^-, K^+ in water samples were similar in all vegetation types. Iron concentration increased from rich to poor fens (Fig. 2), but the differences between vegetation types were not statistically significant. Extremely rich fens are characterized by significantly lower water table than other types of fens (KW-H = 10.51, $P = 0.0147$).

Multivariate analyses

PCA of environmental variables indicated two major gradients, one connected with pH, conductivity, calcium and magnesium concentrations and one with nutrient availability (ammonium, nitrate, potassium). Water table depth is greater in both, nutrient-rich fens and acidic fens. The different types of vegetation were particularly well-separated along the first axis, with the exception of those rich and moderately rich fens that are enriched in nutrients (Fig. 3).

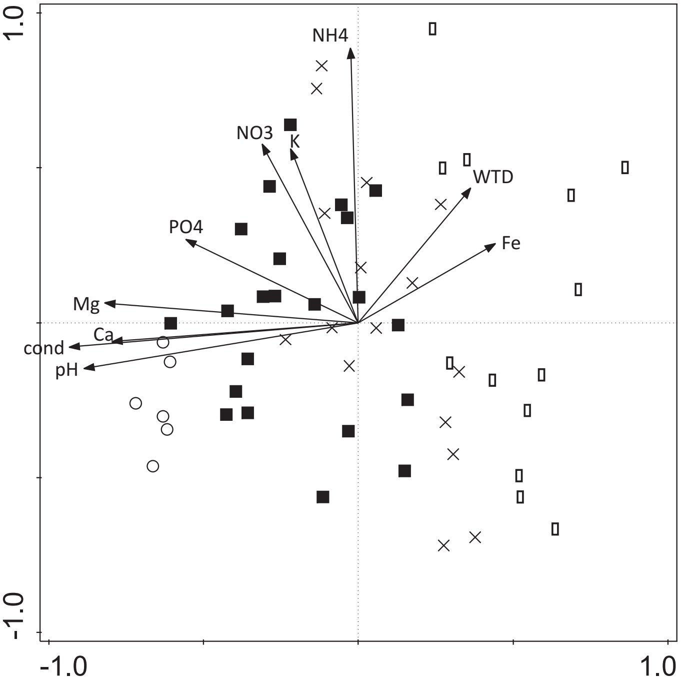
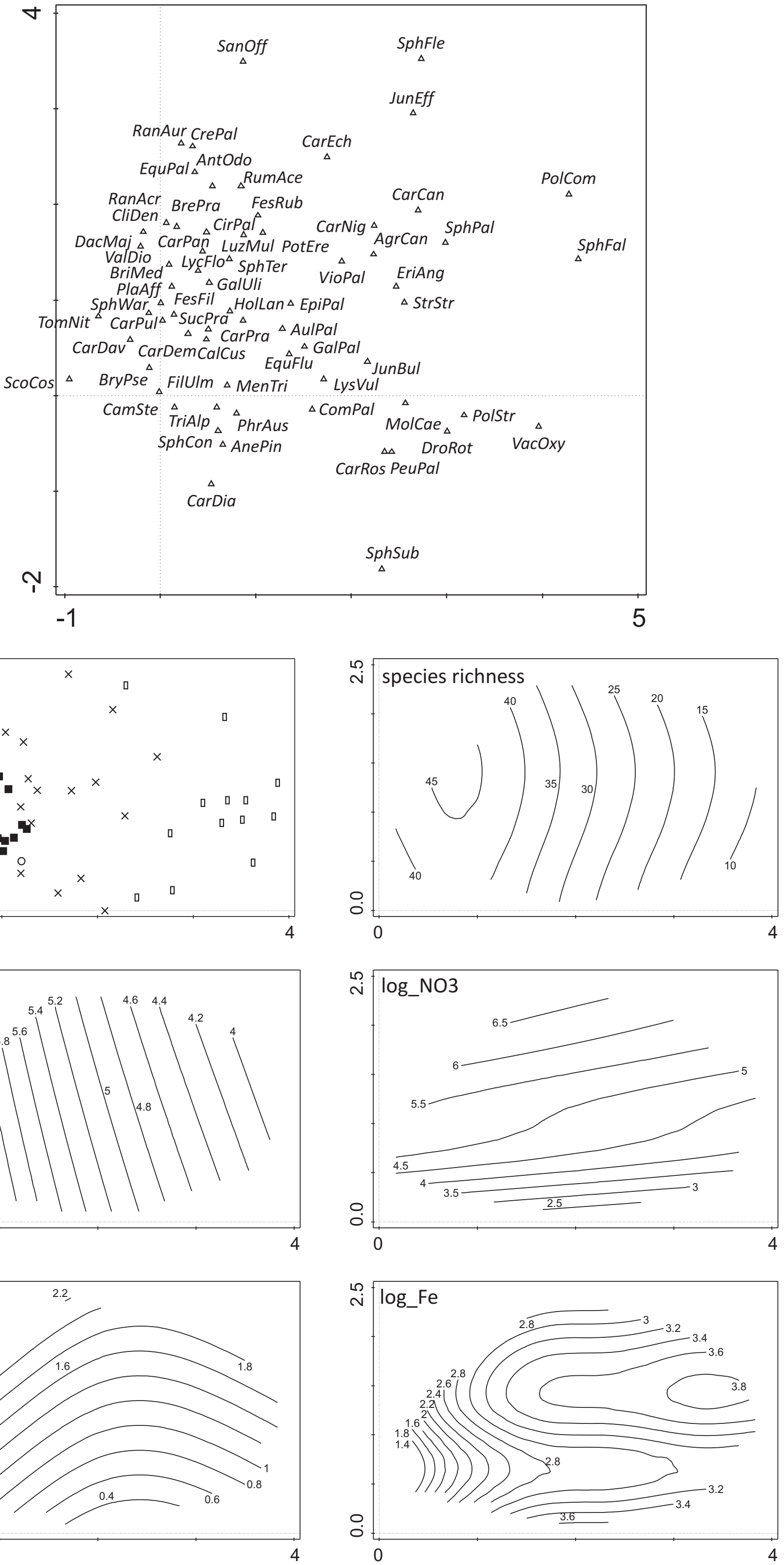


Fig. 3. – PCA ordination of samples based only on environmental variables. Eigenvalues of the first two axes are 0.376 and 0.180. Plots of different vegetation types are indicated by different symbols: ○ *Caricion davallianae* (extremely rich fens), ■ *Sphagno warnstorfii-Tomentypnion* (rich fens), × *Caricion canescenti-nigrae* (moderately rich fens), ▯ *Sphagno-Caricion canescentis* (poor fens).

A simple DCA ordination diagram based on both vascular plants and bryophytes (Fig. 2) indicates that each group (alliance) is clearly separated along the main vegetation gradient (first DCA axis) stretching from extremely rich fens (with *Carex davalliana*, *Tomentypnum nitens* or *Scorpidium cossonii*) to poor fens (with *Polytrichum commune* or *Sphagnum fallax*). The second DCA axis is of minor importance, with less than half the eigenvalue (Fig. 4), and can be interpreted as fen-to-meadow gradient, largely coinciding with the water level gradient) stretching from waterlogged sites with strictly wetland species (e.g. *Carex diandra*, *Sphagnum contortum*, *S. subsecundum*) to plots with broad-leaved herbaceous plants of rather mesic conditions (e.g. *Ranunculus auricomus* agg., *Sanguisorba officinalis*). Water pH significantly decreased along the main vegetation gradient towards poor fens (Fig. 4). A similar result was also recorded for conductivity and both calcium and magnesium concentrations (Table 2, scatters not shown). Concentrations of potassium and nitrates correlated with the second axis. Concentration of total iron in water slightly increased towards the "poor" end of the first axis and towards the "wet" end of the second axis.

Fig. 4. – DCA ordination of all the plots sampled using pooled data on species compositions of both vascular plants and bryophytes. Position of relevés and species along two first ordination axes are shown. The eigenvalues of the axes are 0.475 (12.4% of total inertia) and 0.193 (5.0%). Only the species with a weight above 10% are shown (for full names see Electronic Appendix 3). Plots of different vegetation types are indicated by different symbols: ○ *Caricion davallianae* (extremely rich fens), ■ *Sphagno warnstorfii-Tomentypnion* (rich fens), × *Caricion canescenti-nigrae* (moderately rich fens), ▯ *Sphagno-Caricion canescentis* (poor fens). Isolines of selected environmental variables and species richness along two main vegetation gradients were created using generalized additive models (GAMs). ▶


4
-2
-1
5
SanOff
SphFle
JunEff
RanAur
CrePal
CarEch
EquPal
AntOdo
RumAce
PolCom
RanAcr
BrePra
FesRub
CarCan
CliDen
CirPal
CarNig
SphPal
DacMaj
CarPan
LuzMul
PotEre
AgrCan
SphFal
ValDio
LycFlo
SphTer
BriMed
VioPal
EriAng
PlaAff
GalUli
SphWar
FesFil
HolLan
EpiPal
StrStr
TomNit
CarPul
SucPra
CarPra
AulPal
CarDav
CarDem
CalCus
GalPal
EquFlu
JunBul
ScoCos
BryPse
FilUlm
MenTri
LysVul
CamSte
ComPal
TriAlp
PhrAus
MolCae
PolStr
SphCon
AnePin
DroRot
VacOxy
CarRos
PeuPal
CarDia
SphSub
2.5
0.0
0
4
species richness
40
25
20
15
45
35
30
40
10
pH
5.2
4.6
4.4
5.4
4.2
5.6
4
5.8
6
6.2
6.4
5
4.8
6.6
6.8
log_NO3
6.5
6
5
5.5
4.5
4
3.5
3
2.5
lok_K
2.2
1.6
1.8
2
1
1.4
0.8
1.2
0.4
0.6
log_Fe
2.8
3
3.2
3.4
3.6
2.8
2.6
2.4
3.8
2.2
2
1.6
1.8
1.4
2.8
3.2
3.4
3.6

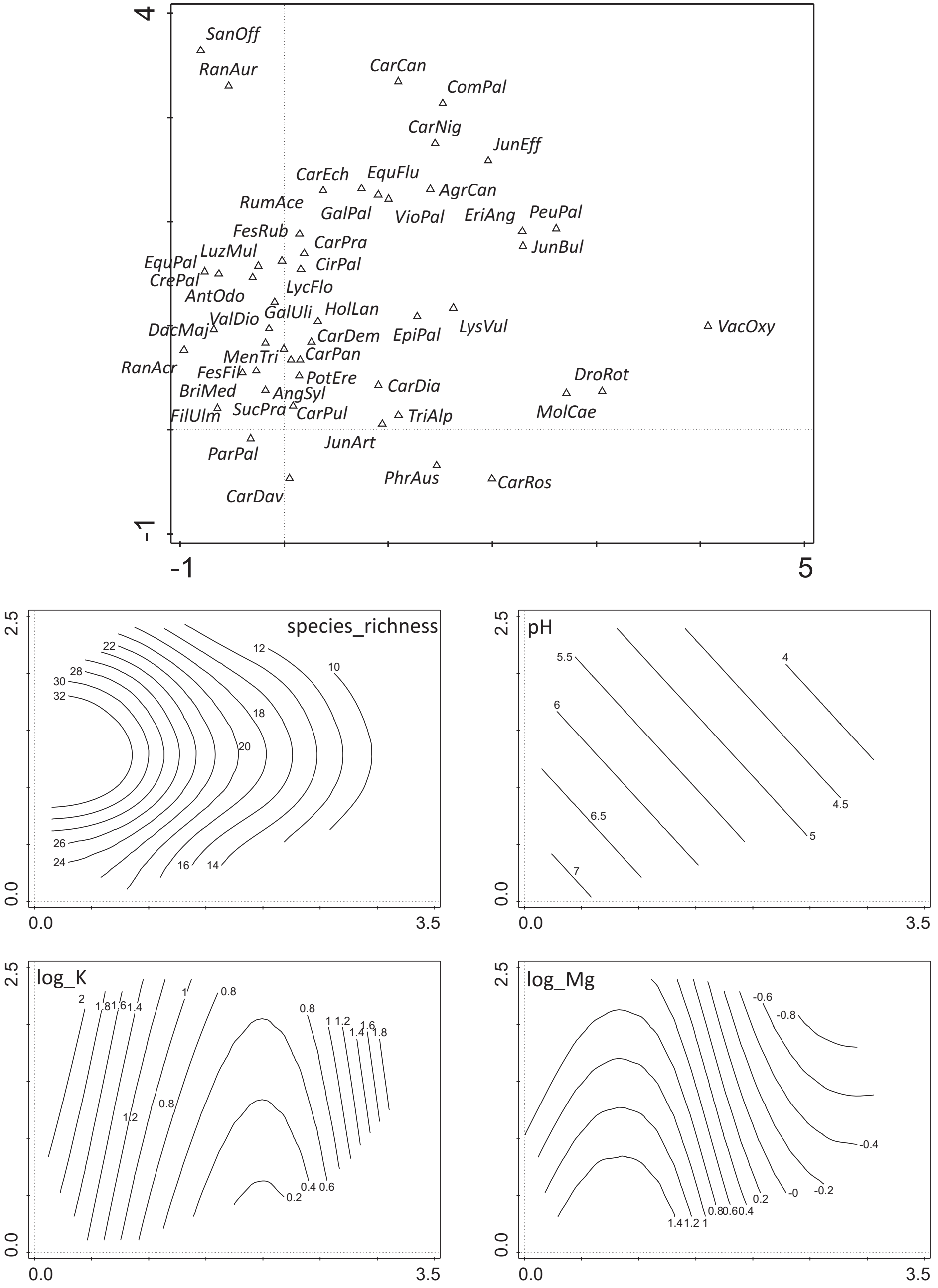


Fig. 5. – DCA ordination of all the plots sampled using only the data on species compositions of vascular plants. Positions of the species along the first two ordination axes are shown. The eigenvalues of the axes are 0.328 (10.0% of total inertia) and 0.208 (6.3%). Only species with a weight above 10% are shown (for full names see Electronic Appendix 3). Isolines of selected environmental variables and species richness along the two main vegetation gradients were created using generalized additive models (GAMs).

Table 2. – The relationships between the two principal DCA ordination axes and environmental variables modelled and tested using generalized additive models. Two significance levels are presented. The unadjusted P-values lower than 0.05 are presented, and those which are significant after the Holm correction ($P < 0.00208$) are indicated by *. The last column describes the axis with which the tested variable coincided.

Species data	Variable	Deviance	DF	F	P	Fitting to axes
Vascular plants + bryophytes	pH	9.2538	4	84.1	< 0.00001*	1st axis (Fig. 4)
	conductivity (log)	11.644	6	24.3	< 0.00001*	1st axis
	Ca^{2+} (log)	22.516	6	13.5	< 0.00001*	1st axis
	Mg^{2+} (log)	24.375	7	10.2	< 0.00001*	1st axis, right-skewed
	PO_4^{3-} (log)	12.413	5	4.7	0.00255	1st axis
	K^+ (log)	47.944	4	6.1	0.00124*	2nd axis (Fig. 4)
	NH_4^+ (log)	38.219	5	3.9	0.00770	2nd axis
	NO_3^- (log)	148.35	5	5.3	0.00109*	2nd axis (Fig. 4)
	total Fe (log)	72.75	7	5.1	0.00038*	both, non-linearly (Fig. 4)
	WTD (log)				not significant	
Vascular plants	pH	13.466	3	71.3	< 0.00001*	diagonally (Fig. 5)
	conductivity (log)	12.361	6	21.8	< 0.00001*	diagonally
	Ca^{2+} (log)	11.119	3	5.1	0.00846	diagonally
	Mg^{2+} (log)	28.641	5	11.3	< 0.00001*	1st axis, skewed (Fig. 5)
	PO_4^{3-} (log)	12.637	6	3.3	0.01143	both, non-linearly
	K^+ (log)	43.42	5	5.4.	0.00110*	1st axis, bimodally (Fig. 5)
	NH_4^+ (log)	38.733	5	2.7	0.03828	both, non-linearly
	NO_3^- (log)	161.95	6	2.9	0.02241	both, non-linearly
	total Fe (log)	94.746	4	3.7	0.01509	both, non-linearly
	WTD (log)	19.053	4	3.6	0.02019	both, non-linearly
Bryophytes	pH	9.9109	5	55.8	< 0.00001*	1st axis (Fig. 6)
	conductivity (log)	9.6566	5	39.2	< 0.00001*	1st axis
	Ca^{2+} (log)	27.708	4	15.3	< 0.00001*	1st axis
	Mg^{2+} (log)	28.474	5	11.5	< 0.00001*	1st axis
	PO_4^{3-} (log)	14.041	3	5.3	0.00724	both, non-linearly
	K^+ (log)				not significant	
	NH_4^+ (log)				not significant	
	NO_3^- (log)				not significant	
	total Fe (log)	89.757	4	5.3	0.00280	1st axis
	WTD (log)	2900.7	7	2.9	0.01753	1st axis

In the DCA of only vascular plant data, the main gradient was dominated by increasing species richness, governed by the representation of grassland species, and coincided with pH only partially. The pH gradient stretches diagonally as a resultant of both the first and the second axis (Fig. 5). Potassium concentration shows a bimodal relationship with the first axis, with maxima at opposite ends of the main gradient: in species-rich fen grasslands and poor fens. The DCA of bryophyte data yielded a much simpler result, with the dominant main axis sorting the species from calcicolous brown mosses (*Tomentypnum nitens*, *Scorpidium cossonii*) to poor-fen species (*Polytrichum commune*, *Sphagnum fallax*), which were tightly linearly correlated with pH (Fig. 6).

The forward selection in the CCA revealed the key role of water pH in the entire data set (explained variance: 39.5%, $F = 5.8$, $P = 0.002$, $P_{adjust} = 0.018$). The residual variance was partially explained by nitrate concentration with marginal significance (expl. var.: 10.3%, $F = 1.6$, $P = 0.008$, $P_{adjust} = 0.064$). The variation within the vascular plant subset was

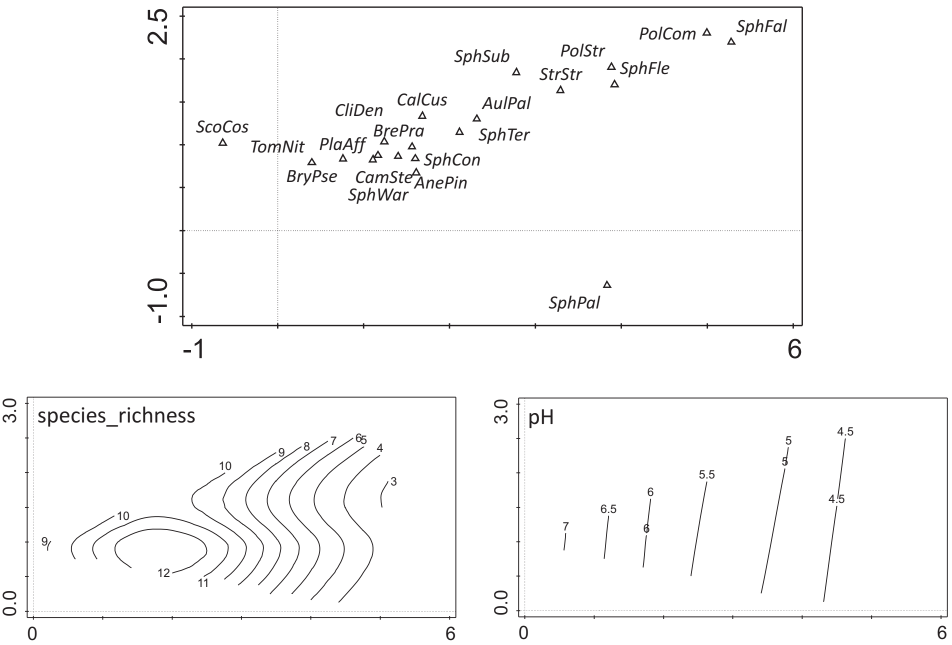


Fig. 6. – DCA ordination of all of the plots sampled using only the data on species composition of bryophytes. Positions of the species along the first two ordination axes are shown. The eigenvalues of the axes are 0.707 (14.9% of total inertia) and 0.345 (7.3%). Only species with a weight above 10% are shown (for full names see Electronic Appendix 3). Isolines of selected environmental variables and species richness along the two main vegetation gradients were created using generalized additive models (GAMs).

mostly determined by pH (expl. var.: 27.2%, F = 3.8, P = 0.002, $P_{adjust} = 0.02$), while nitrate concentration appeared to be the second most important factor (expl. var.: 12.0%, F = 1.7, P = 0.002, $P_{adjust} = 0.02$). In the case of bryophytes, pH explained 47.7% of variance (F = 7.1, P = 0.002, $P_{adjust} = 0.018$) and no other variable was a significant predictor of species composition.

Discussion

The poor-rich gradient within fens on the Bohemian Massif

The floristic composition of mires in the south-eastern part of the Bohemian Massif is associated with differences in pH and concentration of dissolved base cations. This result is not surprising and matches the results of other studies throughout the world (e.g. Malmer 1986, Gerdol 1995, Økland et al. 2001, Hájek et al. 2002), including on parts of the Bohemian Massif (Navrátilová et al. 2006, Laburdová & Hájek 2014). Contrary to the fens in the Carpathian part of the Czech Republic (Hájek et al. 2002), water pH appeared to be more tightly correlated with the main vegetation gradient than calcium concentration. This difference can be explained by the poor-rich gradient in the study area being incomplete due to the absence of calcareous fens and rare occurrence of extremely rich fens. This incompleteness is first of all caused by the prevalence of carbonate-poor rocks and lack of calcareous tufas in both the Bohemian-Moravian Highlands and Třeboň basin (Kovanda 1971). The second reason is the deterioration of the fens due to drainage, fertilization and abandonment and consequent successional changes in these communities. For example, brown-moss fens with boreal sedges (classified as *Drepanoclado revolventis-Caricetum lasiocarpae* and *Scorpidio-Caricetum limosae* in Rybníček et al. 1984) have not been recorded recently in the study area. In addition, this result indicates that water pH is a good proxy of the complex pH/calcium gradient and is similar to the results from other crystalline regions in Europe, such as Fennoscandia (Tahvanainen 2004) and alpine zones of high European mountains (Hájková et al. 2006, Sekulová et al. 2013).

In contrast to previously explored regions (Boyer & Wheeler 1989, Boeye et al. 1997, Rozbrojová & Hájek 2008, Kooijman & Hedenäs 2009), the most calcium-rich habitats (*Caricion davallianae*) were not generally determined by low phosphorus availability. The data from the entire Bohemian Massif did not confirm that the availability of phosphorus in the *Sphagno warnstorfii-Tomentypnion* fens is lower than in poor fens as indicated previously by data from the Carpathians (Hájek et al. 2002) and the Třeboň basin (Navrátilová et al. 2006). Concentration of phosphates in water increased towards high-pH fens in our study area and the N:P ratio in bryophyte biomass indicated a similar level of phosphorus limitation in all vegetation types. Such an important difference from what is recorded in other regions is probably caused by generally rather high concentrations of dissolved iron in the study area, which makes phosphorus unavailable to plants (Zak et al. 2004, Cusell et al. 2013). The lack of coincidence between dissolved phosphorus or nitrogen in the soil water and differentiation of vegetation types along the poor-rich gradient is also evident from the results of PCA of environmental factors, where vegetation types were differentiated along the first (pH/calcium) axis but not along the second, the nutrient-availability axis. Moreover, nutrient-enriched fens with a high score along the second axis were recorded for all vegetation types other than extremely rich fens.

If dissolved nutrients are not associated with the poor-rich gradient on the Bohemian Massif, what factors are responsible for vegetation differentiation along the pH/calcium gradient? In drier habitats, iron unavailability in calcareous soils and high concentration of toxic aluminium in acid soils ($pH < 4.5$) are considered to be a major causal explanation of the calcicole-calcifuge behaviour of species (Zohlen & Tyler 2000, Tyler 2003). On the Bohemian Massif, low pH that enables the mobilization of aluminium occurs only in poor fens, but also other vegetation types were mutually well-differentiated with respect to pH. Iron concentration increased towards poor fens (see also Rozbrojová & Hájek 2008), but differences among different vegetation types were not statistically significant. Moreover, there are very high concentrations of dissolved iron (10–200 $mg \cdot l^{-1}$) throughout the area studied, suggesting iron toxicity (Snowden & Wheeler 1993, Aggenbach et al. 2013) affecting all vegetation types. Hence, iron alone cannot explain the species turnover along the pH/calcium gradient.

If this is the case, what is the ecological explanation of the poor-rich gradient? We suggest that interactions between pH, calcium concentration in the water and water level affect the poor-rich gradient in a complicated way. All these factors determine species composition of vegetation, especially of its moss layer, and mosses are generally recognized to be crucial ecosystem engineers of mires (Jones et al. 1994, Vitt 2000). Clymo (1973) reports a negative up to a lethal effect of rich-fen water (having high pH and a high calcium concentration) on most of the species of *Sphagnum* he studied. Granath et al. (2010) states that inundation of capitula by rich-fen water is lethal for the bog species *Sphagnum fuscum*, but does not affect the calcium-tolerant species *S. teres*. Apart from *S. fuscum*, several other species of *Sphagnum* avoid calcium by forming hummocks (Brehm 1971, Hájek et al. 2014). We conclude that sphagna are generally intolerant of an elevated water table in calcium-enriched fens. Thus, the combination of pH with calcium and water level determines whether a fen will be dominated by either sphagna or brown mosses, or both. Sphagna and brown mosses may affect ecosystem processes differently. Sphagna acidify the environment (Kooijman 2012) and drive the succession towards poor fens (Paulissen et al. 2013), take up most nutrients (Malmer et al. 1994, Fritz et al. 2014), hamper seed germination or seedling establishment (Neuhäusl 1975, Soudzilovskaia et al. 2011) and decrease decomposability of organic matter and hence nutrient mineralization (Hájek et al. 2011a). Great competitive ability of *Sphagnum* species can result in competitive exclusion of some vascular plants and a decrease in species richness (Hájková & Hájek 2003, Malmer et al. 2003, van der Welle et al. 2003). On the other hand, hummock-forming calcium-tolerant sphagna may provide a specific niche for shallow-rooting vascular plants that may avoid iron toxicity and reducing conditions by growing in aerated but permanently wet *Sphagnum* hummocks. Ecosystem role of brown mosses is less well known, but some studies indicate they have a specific role in nutrient cycling and uptake by plants by affecting redox conditions (Crowley & Bedford 2011). In conclusion, we suggest that pH differences in fens control the occurrence of particular species of moss, which may act as ecosystem engineers and regulate the vegetation structure to which phanerogamic species respond. Some short-lived vascular plants tightly associated with calcareous fens may not be calcium-demanding, but just cannot reproduce generatively in dense *Sphagnum* carpets.

Other gradients

The poor-rich gradient is commonly identified as the main vegetation gradient in fens, but not always. Floristic and faunistic composition of Polish lowland fens, is, for example, more affected by factors connected with hydrology and phosphorus availability (Pawlikowski et al. 2013, Schenková et al. 2014). We expected an increasing role of hydrology and nutrient availability in our data set, which contains floristically unique topogenic fens and fens eutrophicated by polluted water (Navrátilová et al. 2006), and fens naturally enriched by potassium from weathering feldspars on granite bedrock. In comparison with the data reported for fens in the literature (Sjörs 1948, Malmer 1962, Persson 1962, Mörnsjö 1969, Elveland 1976, Zoltai & Vitt 1995, Wind-Mulder et al. 1996, Hájek et al. 2002, Hedenäs & Kooijman 2004, Tahvanainen 2004, Pawlikowski et al. 2013), groundwater in the study area contains generally more potassium and iron. Similar concentrations of potassium (up to 20 $mg \cdot l^{-1}$, with a mean value of about 5 $mg \cdot l^{-1}$) are reported only by Gąbka & Lamentowicz (2008) for poor fens in western Poland. Also phosphate concentration in groundwater in the study area is substantially higher than in Scandinavia (Mörnsjö 1969, Hedenäs & Kooijman 2004), slightly higher than that recorded in the Outer Western Carpathians (Hájek et al. 2002), much higher than in the Inner Western Carpathians (Hájek et al. 2014) but similar to the concentration in north-eastern Poland (Pawlikovski et al. 2013). Despite these differences, the gradient structure fits the general pattern found across temperate Europe, i.e. primary gradient of pH and calcium and secondary gradient of fertility (Gerdol 1995, Wheeler & Proctor 2000, Hrivnák et al. 2008). In contrast in the Western Carpathians where absolute concentrations of nutrients in water are less important than stoichiometry (compare Hájek et al. 2002, Hájek & Hekera 2004 and Rozbrojová & Hájek 2008), the fertility gradient on the Bohemian Massif coincided with the absolute concentrations of particular nutrients, especially potassium and nitrate. It is partially correlated with water table depth, because water table decline causes nutrients in peat to mineralise (Grootjans et al. 1986). Water table depth further correlates with pH, because acidic fens may develop from alkaline fens after a water table decline that isolates the fen surface from the effect of groundwater (Granath et al. 2010, Paulissen et al. 2013).

The complex gradient of fertility and water table depth (the fen-to-meadow gradient) was, however, much more strongly pronounced in vascular plant data. The result of a more complex control of vascular plant distribution in fens, including nutrient availability, is in accordance with results from the Western Carpathians (Hájková & Hájek 2004), Canada (Vitt & Chee 1990), the Netherlands (van Baaren et al. 1988) and the Alps (Bragazza & Gerdol 2002, Miserere et al. 2003, Sekulová et al. 2013).

Implications for fen classification

Four vegetation types distinguished in this study matched the classification of central-European minerotrophic mires proposed by Hájek et al. (2006), which follows the tradition of Scandinavian mire ecologists (Nordhagen 1943, Malmer 1986, Sjörs & Gunnarsson 2002). In other words, the main fen vegetation types (alliances) on the Bohemian Massif correspond to parts of the poor-rich gradient and clearly differ from each other in species composition and site conditions. Water conductivity, calcium concentration and most importantly pH seem to be the variables best reflecting the floristic delimitation of particular vegetation types. Bryophytes were found to play an important role in vegetation diversification, because they mainly reflect a single dominant gradient of water pH and calcium. Moreover, they play a crucial role in mire ecosystem functioning and via direct interactions with vascular plants they affect the overall species composition of fen vegetation. The Scandinavian classification system delimiting major types of fens according to base saturation and associated structure of the bryophyte layer, thus appeared to be more suitable for our study area than the German-Austrian system based on hydrological gradients and dominance of particular vascular plants such as *Rhynchospora alba*, *Carex lasiocarpa*, *C. limosa*, *C. nigra* or *Menyanthes trifoliata* (Koch 1926, Oberdorfer 1957, Dierssen 1982, Steiner 1992), but nevertheless it is applied to fens in the Austrian part of the Bohemian Massif (Zechmeister & Steiner 1995).

We aimed initially to address the specific question of floristic and environmental delimitation of the *Sphagno warnstorfii-Tomentypnion* fens that are currently disappearing but are extremely important in terms of biodiversity conservation. We conclude that our results confirm the meaningfulness of distinguishing the *Sphagno warnstorfii-Tomentypnion* alliance, which was clearly differentiated based on both its floristic composition and water chemistry in our study. It further formed a quite compact cluster in the DCA ordination diagram. The presence of habitat specialists and rare and endangered species is high, which conforms with results from the Western Carpathians and Bulgaria (Hájek et al. 2007). High species richness together with a high representation of habitat specialists suggests continuity over longer periods of time in the study area (compare Hájek et al. 2007). Thus the *Sphagno warnstorfii-Tomentypnion* fens can be characterized as mineral-rich fens where either a slight decrease in the water table, or suitable pH and calcium levels, enable the co-occurrence of calcium-tolerant sphagna (*Sphagnum warnstorfii*, *S. contortum*, *S. teres*, *S. subnitens*) with boreal species of brown mosses. They are rich in habitat specialists, with a group of shallow-rooting boreal fen plants. In the boreal zone these fens are more widespread but poorer in grassland species and calcareous-fen specialists than in central Europe. Similar alliances occur in European Russia and Siberia (Smagin 1999, 2007, Lapshina 2010). The variation in the *Sphagno warnstorfii-Tomentypnion* alliance on a European scale thus deserves further research.

See www.preslia.cz for Electronic Appendices 1–3

Acknowledgements

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Souhrn

Jihovýchodní část Českého masivu (Českomoravská vrchovina, Třeboňsko) je významným centrem slatinné vegetace a její biodiverzity. Ohrožené druhy rostlin a živočichů zde hostí zejména slatiniště svazu *Sphagno warnstorfii-Tomentypnion*, jejichž prostředí představuje specifický úsek gradientu pH a vápnitosti, který je nejvýznamnějším gradientem uvářejícím druhové složení rašelinišť. Floristické a ekologické vymezení hlavních vegetačních typů (svazů) podél tohoto gradientu, od chudých (přechodových) slatinišť po vápníkem bohatá slatiniště, bylo dosud testováno zejména na datech ze Západních Karpat a Bulharska. Tyto studie nelze jednoznačně extrapolovat na území Českého masivu, kde jsou častá topogenní rašeliniště a kde podzemní voda obsahuje celkově více draslíku, železa a fosforu než v jiných oblastech Evropy. Aktuální vegetační přehledy sousedních zemí sdílejících části Českého masivu (Rakousko, Německo, Polsko) vymezení hlavních typů rašelinné vegetace podle komplexního gradientu pH/vápnitosti nepřijímají a svaz *Sphagno warnstorfii-Tomentypnion* tedy nerozlišují. V této studii jsme shromáždili data o vegetaci a proměnných prostředí (chemismu vody a hloubce vodní hladiny) z 57 unikátních zachovalých slatinišť. Klasifikace získaných fytocenologických snímků pomocí algoritmu ISOPAM téměř beze zbytku odpovídala vymezení svazů v monografii Vegetace ČR. Jednotlivé vegetační typy byly téměř odděleny v analýze hlavních komponent, která zohledňovala jen data o prostředí. Všechny vegetační typy se vzájemně signifikantně lišily v pH vody, jehož hodnoty, stejně jako koncentrace vápníku ve vodě, korelovaly s hlavním vegetačním gradientem vyjádřeným první osou detrendované korespondenční analýzy. Podél druhé osy, představující sekundární vegetační gradient, se měnila koncentrace dusičnanů a fosforu. Ordinační analýzy ukázaly poněkud odlišné výsledky, když byla společenstva mechorostrů a cévnatých rostlin analyzována odděleně. Analýza společenstev mechorostů nevytvořila sekundární gradient spojený s přístupností živin a analýza společenstev cévnatých rostlin vytvořila primární gradient, který odrážel vzrůstající počet druhů, včetně generalistů, od chudých k velmi bohatým slatiništím a jen částečně koreloval s pH. Oproti našemu očekávání nebyla bohatá slatiniště svazu *Sphagno warnstorfii-Tomentypnion*, ani vápníkem bohatá slatiniště svazu *Caricion davallianae*, vymezena nízkou dostupností fosforu, jako tomu bylo v jiných studiích ze střední Evropy. Druhové složení nejvápnitějších slatin tedy pravděpodobně určuje vysoké pH a velká koncentrace vápníku, vysoká hladina podzemní vody a možná i nízká koncentrace přístupného železa. Velká alkalinita vede spolu s trvalým zamokřením k absenci rašeliníků a umožňuje tak výskyt některých kompetičně slabých druhů cévnatých rostlin, které nejsou vždy a priori vápnomilné, ale nemohou se generativně množit v souvislých porostech rašeliníků. Naše data ukazují, že

vymezení hlavních vegetačních typů (svazů) rašelinné vegetace podél gradientu pH a vápnitosti má značný floristický i ekologický smysl také v hercynských pohořích a že výskyt jednotlivých vegetačních typů je předurčen zejména úrovní pH a koncentrací vápníku v prostředí. Uvedené faktory přímo ovlivňují výskyt jednotlivých funkčních skupin mechorostů, které pak rozhodujícím způsobem ovlivňují jak výskyt jednotlivých druhů cévnatých rostlin, tak i fungování rašelinného ekosystému jako celku.

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