Changes in the moss layer in Czech fens indicate early succession triggered by nutrient enrichment

Změny v mechovém patře českých slatinišť indikují časnou fázi sukcese vyvolanou obohacením o živiny

Michal Hájek[1], Martin Jiroušek[1,2], Jana Navrátilová[1,3], Eliška Horodyská[1,4], Tomáš Peterka[1], Zuzana Plesková[1], Josef Navrátil[5], Petra Hájková[1,6] & Tomáš Hájek[3,7]

[1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic, e-mail: hajek@sci.muni.cz, jirousek@mendelu.cz, janaernestova@seznam.cz, eliska.horodyska@nature.cz, peterkatomasek@seznam.cz, pleskovicova@gmail.com, buriana@sci.muni.cz; [2]Department of Plant Biology, Faculty of Agronomy, Mendel University in Brno, Zemědělská 1, CZ- 613 00 Brno, Czech Republic; [3]Department of Functional Ecology, Institute of Botany, The Czech Academy of Sciences, Dukelská 135, CZ-379 82 Třeboň, Czech Republic, e-mail: tomas.hajek@prf.jcu.cz; [4]Department of Species Protection, Nature Conservation Agency of the Czech Republic, Kaplanova 1931/1, CZ-148 00 Praha 11 – Chodov, Czech Republic (present address); [5]Department of Biological Studies, Faculty of Agriculture, University of South Bohemia in České Budějovice, Studentská 13, CZ-307 05 České Budějovice, Czech Republic, e-mail: jnav@centrum.cz; [6]Department of Vegetation Ecology, Institute of Botany, The Czech Academy of Sciences, Lidická 25/27, CZ-657 20 Brno, Czech Republic; [7]Department of Experimental Plant Biology, Faculty of Science, University of South Bohemia in České Budějovice, Branišovská 1760, CZ-370 05 České Budějovice, Czech Republic

Hájek M., Jiroušek M., Navrátilová J., Horodyská E., Peterka T., Plesková Z., Navrátil J., Hájková P. & Hájek T. (2015): Changes in the moss layer of Czech fens indicate early succession triggered by nutrient enrichment. – Preslia 87: 279–301.

Temperate fens are rapidly losing their specialized species. This applies even to seemingly untouched fens, in which the moss layer in particular is undergoing rapid succession. We analysed historical and recent vegetation-plot data from fens in the agricultural landscape on the Bohemian Massif (Czech Republic) to test the hypotheses that (i) more acidicolous and/or competitively stronger species that benefit from increased nutrient availability regionally increase in frequency and in percentage cover, and (ii) these competitively stronger bryophytes have become more tolerant of high pH because of the increased nutrient supply. We worked with two datasets: a precise dataset (the most similar pairs of samples from the same fens) and a large dataset (all of the historical and recent samples from the area studied). We found that calcicolous brown mosses specialized for growing in fens have recently been retreating to places with the highest pH, being replaced by more nutrient-demanding species such *as Calliergonella cuspidata*, *Sphagnum palustre*, *S. teres* and *Straminergon stramineum* in most of rich fens. *Sphagnum fallax* and *S. flexuosum* spread only in poor fens. At the level of individual species, the intensity of change in species abundance (cover-weighted frequency change) correlated significantly with the median potassium concentration in the biomass of species based on a large set of recent data. We conclude that nature conservancy authorities should monitor changes in the species composition of the moss layer as this may signal the initial phase of nutrient enrichment of seemingly intact fens in agricultural landscapes.

Keywords: bryophytes, decline of threatened species, mire, nutrients, pH, vegetation change

Introduction

Many habitats in human-affected landscapes are currently experiencing a substantial loss of biodiversity (Butchart et al. 2010, Dullinger et al. 2013). This generally accepted fact contrasts with the previous Holocene development, during which the effect of human activities resulted in a more diversified landscape (Feurdean et al. 2010, Colombaroli & Tinner 2013), provided refuges for light-demanding species during the forest optimum (Hájková et al. 2011b, 2013) and even created new habitats such as open fen grasslands rich in rare and specialized plants (Moravec & Rybníčková 1964, Hájková et al. 2012, Jamrichová et al. 2014). Fens scattered across arable land, managed grasslands or forests, are among the most rapidly deteriorating habitats because of drainage, peat extraction and cessation of management (Fojt & Harding 1995, Jensen & Schrautzer 1999, Bollens et al. 2001, Diemer et al. 2001, Grootjans et al. 2005, Mälson et al. 2008, Graf et al. 2010, Koch & Jurasinski 2014, Seer & Schrautzer 2014, Pasquet et al. 2015). This trend is occurring throughout Europe. As the disturbing factors, such as drainage, adversely affect the conditions necessary for the occurrence of species specialized to fens, successional changes are to be expected. A greater challenge is to understand why many seemingly untouched fens in central Europe, which still retain their sedge-moss fen vegetation, have recently lost much of their species diversity. Bergamini et al. (2009) report the loss of habitat specialists in Swiss calcareous fens despite conservation management between 1995 and 2006. Deterioration of other individual Swiss fens caused by eutrophication, desiccation or both is reported also by other authors (Bollens et al. 2001, Küchler et al. 2009). Rapid successional changes have occurred in Dutch fens (Kooijman 2012, Paulissen et al. 2014), and loss of some fen species, especially bryophytes, is reported for many central-European (Zechmeister et al. 2002, Štechová & Kučera 2007, Štechová et al. 2010, 2012) and even boreal regions (Gunnarsson et al. 2000, Heino et al. 2005, Juutinen 2011, Kapfer et al. 2011). In most of these studies, changes are recorded in the bryophyte layer in terms of a decline in so-called brown mosses (i.e. non-sphagnaceous fen genera such as *Drepanocladus*, *Scorpidium*, *Hamatocaulis*, *Meesia* and *Paludella*), calcium-tolerant peat mosses (*Sphagnum warnstorfii*, *S. contortum*) and an increase in calcifuge peat mosses or other late-successional acidicolous mosses. As a consequence, some regional vegetation surveys report the regional disappearance of certain types of fen vegetation associated with the dominance of brown mosses and calcicolous species; their authors hypothesize that this has resulted in an increase in poor fens dominated by calcifuge peat mosses (Hájek et al. 2002, Horodyská 2006, Navrátilová et al. 2006, Navrátil & Navrátilová 2007, Peterka et al. 2014). Thus, undesirable successional changes in fens may be well indicated by changes in the species composition of the moss layer.

Only a few studies record changes in the moss layer in otherwise untouched fens or address the causes of this process. So far, the only country where the causes of this process have been studied in detail is the Netherlands. Kooijman (2012) concludes that two processes are responsible for the ongoing shift in vegetation. First, drainage causes rainwater to accumulate in the moss layer, which leads to the replacement of brown mosses by the peat moss *S. subnitens* and later *S. fallax*. The second process, which may act independently or synergistically with the first, is nutrient enrichment that leads to replacement of fen brown mosses by *Calliergonella cuspidata* and later by *S. squarrosum.* The latter drives succession towards fens with *S. palustre* and *S. fallax*. It is difficult to stop this process because re-irrigation of fens often leads to eutrophication (Cusell et al. 2013). At least local drainage of fens is recorded also in above-mentioned Swiss (Bollens et al. 2001, Bergamini et al. 2009) and Finnish (Heino et al. 2005) fens and springs. A lowering of the water table results in peat mineralization and nutrient release. On the other hand, Scandinavian mires, although not artificially drained, tend to be drier, more acidic and nutrient-rich (Gunnarsson et al. 2000, Kapfer et al. 2011). It is difficult to disentangle the effects of atmospheric nutrient deposition, other sources of eutrophication, autogenic succession and climate change. Kapfer et al. (2011) acknowledge the effect of atmospheric deposition, while Moradi et al. (2012) explicitly attribute the loss of habitat specialists in Swiss fens to ongoing climate warming. By analogy, Essl et al. (2012) drew attention to the fact that a decrease in spring and summer precipitation may pose a threat to fen ecosystems in general.

Considering the likely complexity of these changes, there is still insufficient knowledge about species' dynamics within archipelagos of untouched fen islands in agricultural regions of Europe. The problem is that very few permanent plots were established before the period of large-scale transformations of hydrological regimes and widespread eutrophication. Authors dealing with rapidly changing Dutch fens (see Kooijman 2012 for review) addressed this problem by carrying out physiological or mesocosm experiments. However, the results of small-scale manipulative experiments are difficult to extrapolate to landscape level. Changes occurring at the landscape level have been repeatedly recorded by comparing historical and recent vegetation-plot records (e.g. Fojt & Harding 1995, Bollens et al. 2001, Koch & Jurasinski 2014). Chytrý et al. (2014) demonstrate, using simulation analyses based on existing permanent plot data, that using historical non-permanent plots may falsely indicate significant changes in vegetation. In contrast, Kopecký & Macek (2015) demonstrate that for forests a resurvey of historical vegetation plots may not be affected by non-permanent plot location and hence provide reliable evidence of decadal changes in plant communities. Paulissen et al. (2014) use database data for pre-defined plant associations to determine changes in local frequencies of particular species of fen moss between 1940 and 1999. Although they confirmed certain of the results of both experimental and field studies (e.g. a decline in *Scorpidium scorpioides*, *Campylium stellatum* or *Fissidens adianthoides*) their findings did not confirm all of them. The threatened species, *Calliergon giganteum* and *Sphagnum contortum*, increased in frequency, while *Calliergonella cuspidata*, which increases in Dutch fens (Kooijman 2012), decreased. These results illustrate the possible effect of both different sampling strategies at the landscape level and uneven sampling within particular types of vegetation at different times.

The indirect approach to describing vegetation dynamics using a historical database is based on changes in species' optimum values for different environmental gradients, which makes it less likely to be biased by the position of non-permanent plots (Kapfer et al. 2011). In this study, we used the species-based approach to test the hypothesis that brown-moss fens are turning into *Sphagnum* fens on the Bohemian Massif (Czech Republic) and explore the possible role of increasing nutrient availability in this process. On the Bohemian Massif, endangered species of mosses have disappeared from fens that were never drained nor experienced a change in management. As in the Dutch fens mentioned above, an increase in *Sphagnum* is recorded in many rich fens, especially those enriched by phosphorus, potassium or both (Hájek et al. 2002, 2014, Navrátilová et al. 2006). Because Kooijman & Kanne (1993) and Kooijman & Paulissen (2006) experimentally demonstrate that enhancing the nutrient supply seems to compensate for the intolerance of acidicolous *S. fallax* of high mineral levels, and Vicherová et al. (2015) have shown that potassium slightly compensates for *Sphagnum's* intolerance of calcium, we hypothesize that increasing nutrient supply increases the tolerance of acidicolous peat mosses of high pH and calcium under field conditions. If increasing nutrient availability is causing the recorded successional changes from brown-moss to *Sphagnum* fens, then individual species' optima or amplitudes in terms of pH should change. In addition, the species that increase in abundance should be more competitive under these conditions than stable or declining species and hence require higher nutrient (especially potassium) tissue concentrations in order to grow rapidly (Hájek et al. 2014). To address this second hypothesis, we considered the premise that the concentration of nutrients in tissues is a species-specific trait that, at least in part, reflects the ecological requirements of species (Hájek et al. 2014). We therefore looked for a correlation between the intensity of a species' dynamics and its median biomass concentrations of nitrogen, phosphorus and potassium (obtained from Hájek et al. 2014). To do the above, we created two datasets of historical and recent vegetation-plot records supplemented by measurements of pH: (1) a small (precise) dataset compensated for spatial mismatch between old and new plots; and (2) a large dataset compensated for a low number of replicates.

Materials and methods

Study area

As our study area, we selected the south-eastern part of the Bohemian Massif in the Czech Republic (the Bohemian-Moravian Highlands and Třeboň basin; Fig. 1). This region is an important but deteriorating hotspot of central-European fen biodiversity (Peterka et al. 2014). In terms of their vegetation, fens in this region have been intensively studied since the 1950s–1960s (Březina et al. 1963, Rybníček 1970, 1974). Despite drainage and other management activities undertaken since the 1970s (Růžička 1989), some fens still harbour highly endangered vascular plants such as *Carex chordorrhiza*, *C. dioica*, *C. limosa* and *Trichophorum alpinum* (Navrátilová & Navrátil 2005a), bryophytes such as *Hamatocaulis vernicosus*, *Meesia triquetra*, *Paludella squarrosa* and *Scorpidium scorpioides* (Štechová et al. 2010, 2012) and invertebrates such as the glacial relict snails *Vertigo geyeri* and *V. liljeborgii*, which are extremely rare in temperate Europe (Schenková et al. 2013). There are many widely distributed and diverse fens in this region (see distribution maps of fen plant associations in the Czech Republic in Hájek & Hájková 2011).

The Bohemian Massif is a large crystalline massif stretching over western and central Czech Republic, eastern Germany, southern Poland and northern Austria. The geological substrate of the Bohemian-Moravian Highlands mostly consists of crystalline rocks of proterozoic and paleozoic age, i.e. of different kinds of gneiss, migmatite, granite, granodiorite and phyllite with small bodies of amphibolites, marbles, serpentinites and erlans. Calcium-rich Cretaceous sandstones and claystones occur locally in the so-called "Dlouhé meze" area. The Bohemian-Moravian Highlands belong to the cold-temperate

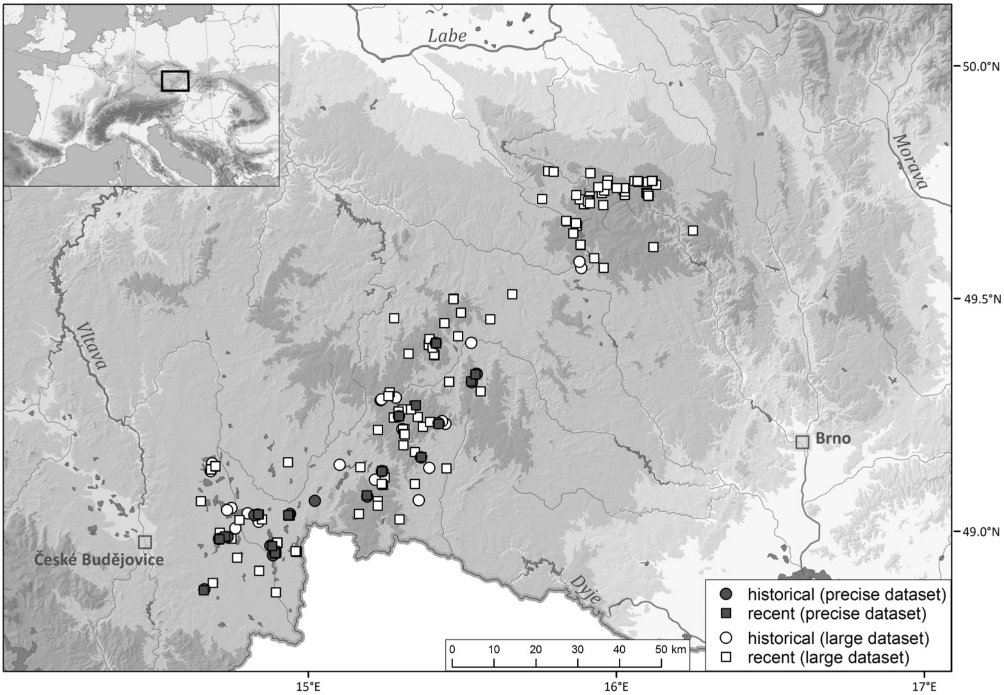


Fig. 1. – Map showing the geographical location of the fens studied. All historical vegetation plot records are indicated by circles and recent ones by squares. Solid symbols refer to the precise dataset.

climatic region with a mean annual temperature of 5.0–6.5 °C and mean annual precipitation of 600–900 mm. The altitudes of the fens investigated range from 450 to 730 m a.s.l. The geological bedrock of 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. Most of the fens are located between 410 and 480 m a.s.l.

Fen terminology

In this study, we use the terms ‘poor fens’ and ‘rich fens’, which differ in water pH with a threshold of pH 5.0 (see the next chapter for reasoning). This terminology was established by Scandinavian authors around mid-20th century (du Rietz 1949). It referred originally to the number of habitat specialists, but these habitats are differentiated also by total species richness, pH and total richness of minerals, especially calcium, but not always by macronutrients (Peterka et al. 2014). By analogy, Wheeler & Proctor (2000) also use a pH threshold of 5.5 to differentiate rich fens from other types of mires.

Creation of datasets

The use of historical data must always take into consideration that large database datasets are likely to be affected by spatial mismatches between old and new plots. Alternatively, using a more precise datasets composed of data from the same fens or at least the same habitats is constrained by the low number of replicates. To utilize the advantages of both these methods, we used two such datasets: one large, which included all available data for target types of vegetation from a wide pre-defined region, and a small yet more precise dataset, which only contained data from the same fens and even the same habitat within these fens. The small (precise) dataset was a subset of the large one. In most analyses, we omitted rare bryophytes and included only the 20 most frequent species/aggregates. These taxa had an absolute frequency higher than 35 in the large dataset and higher than 5 in the subset of historical relevés.

In the first step, we prepared a dataset of vegetation plot records (relevés) for all fens (*Scheuchzerio palustris-Caricetea fuscae* class) in the study area. We divided the dataset into two time periods (1953–1967 and 2002–2013), which includes when most of the relevés were carried out and correspond to the periods before and after the most intense alteration of this landscape during communist times in the 1970s and 1980s (fertilization, peat harvesting and drainage). We refer to relevés from these periods as 'historical' and 'recent', respectively. The historical data came from the publications of Březina et al. (1963) and Rybníček (1970, 1974). These authors collected particular data with the aim of characterizing the different vegetation types occurring in the region. For this purpose the different vegetation types were described in terms of classical phytosociology based on subjectively selected homogenous patches considered as typical, which often meant there was a high concentration of habitat specialists within the plots. Relative species abundances were estimated using Braun-Blanquet cover codes. Water pH was measured in the field in shallow bore holes using a glass-calomel electrode. Plot size varied between 2 and 100 m^2 (most frequently 25 m^2 in 37% of cases). Recent data were collected by Horodyská (2006), Navrátilová & Navrátil (2005b) and during our recent research (Peterka et al. 2014; E. Horodyská, J. Navrátilová & J. Navrátil, unpublished data). During our field research, which began in 2002, we determined the precise location of the fens described in the publications of Březina et al. (1963) and Rybníček (1970, 1974). In the case of fens sampled for the historical dataset their exact locations were provided by K. Rybníček. Relevés were sampled preferentially with the aim of again finding homogeneous patches with a strong presence of habitat specialists, which most closely resembled the historical relevés. At each fen, we usually recorded multiple relevés of the particular types of vegetation recorded in historical studies and reduced the number of relevés later (see below). Relative species abundances were again estimated using Braun-Blanquet cover codes. Water pH was measured in shallow bore holes using portable instruments. Plot sizes were 9–50 m^2 (most frequently 16 m^2 in 75% of cases). The mean number of bryophytes did not differ substantially between the datasets. The mean value for historical plots was 6.63 species and for recent plots 6.77 species. Therefore, we believe that the smaller plot sizes have not substantially affected our results.

Finally, we selected 387 plots located at a total of 140 fens, in which bryophytes were identified and pH measured. In the second step, we assembled two datasets. The large dataset included 75 historical and 312 recent relevés. The second dataset, referred to as the precise dataset, was a subset of the large dataset and contained only 31 pairs of relevés from the same fens, i.e. the same number of plots for each time period (Fig. 1). Whenever more relevés were available for the same fens, the pairs of relevés were selected based on the following criteria: (i) similarity in the pH recorded in the recent and historical relevés and (ii) similarity in species composition (including both vascular plants and bryophytes) using the Jaccard dissimilarity value. This floristic criterion, resulting in more conservative results, was necessary to avoid a false change in vegetation caused by a non-permanent plot position (Hédl 2004, Chytrý et al. 2014).

For analysing changes in cover and frequency of bryophytes, we divided both datasets into pH classes and analysed them separately. This step was necessary in order to down weight changes caused by sampling different habitats (poor fens vs rich fens) in the two periods. Because the precise dataset is based on a lower number of replicates and the main expected change is in the realized niche of acidicolous (poor-fen) vs calcicolous (rich-fen; mostly so called brown-moss-) species, we finally decided to use only two pH classes with the pH threshold set at 5. There were 18 historical and 131 recent plots in the subset of poor fens and 57 historical and 181 recent plots in the subset of rich fens in the large dataset. For the precise dataset, we finally worked with 11 historical and 9 recent plots in the subset of poor fens and 20 historical and 22 recent plots in the subset of rich fens. In the historical dataset, habitats with a pH below or equal 5 are poor fens dominated by poor-fen peat mosses (*Sphagnum fallax*, *S. papillosum*) and virtually without brown mosses. Below pH 5, factors that naturally suppress calcium-tolerant brown mosses, such as aluminium, iron and ammonium toxicity may occur (Paulissen et al. 2005, Lamers et al. 2015), and brown mosses are therefore subject to strong competition from acidicolous poor-fen peat mosses. On the other hand, brown mosses (especially *Scorpidium revolvens* agg., *Breidleria pratensis* and *Calliergonella cuspidata*) occur frequently in fens with a pH above 5. We attempted to analyse the dataset using multiple pH classes, but the same results were recorded for all the pH classes above 5.

Nomenclature and identification of shortcomings

The nomenclature follows Danihelka et al. (2012) for vascular plants and Kučera et al. (2012) for bryophytes. In the historical dataset, *S. recurvum* var. *amblyphyllum* and *S. r.* var. *apiculatum* were interpreted as *S. flexuosum* and *S. fallax*, respectively. *Sphagnum angustifolium* (*S. recurvum* var. *parvifolium*) was not present in the historical dataset, so this species was not included in the analysis. The same constraint applies to *S. centrale*, which was not present in the historical dataset, so we merged *S. palustre* and *S. centrale* into *S. palustre* agg. By analogy, the historical and most of the recent data did not distinguish between *Campylium stellatum* and *C. protensum,* taxa only recently distinguished at the species level (Hedenäs 2003). We therefore merged them into one group referred to as *C. stellatum* agg. Species of the genus *Plagiomnium* (*P. affine*, *P. elatum* and *P. ellipticum*) were merged into *P. affine* agg. Unfortunately, we were unable to distinguish between *Scorpidium revolvens* s.s. and *S. cossonii* in the historical dataset, so we analysed these species at the level of *S. revolvens* agg. *Scorpidium revolvens* s.s. is currently very rare in the Czech Republic (Kučera 2005, Kučera et al. 2012), with few unequivocally identified populations. Nevertheless, because we could not exclude the occurrence of this species in the past, we kept this possibility in mind when interpreting the results (see Discussion).

Water and biomass chemistry

Water pH, standardized at 20 °C, was measured in situ using portable instruments. We repeated the measurements used in the historical research, i.e. measuring in shallow bore holes across the vegetation plots on the same date as the vegetation was sampled. Water pH is one of the most stable environmental parameters in mires, accurately characterizing a site even when spot sampling is used (Hájek & Hekera 2004, Jiroušek et al. 2013).

We used the median concentrations of the main nutrients (nitrogen, phosphorus and potassium) in moss tissue in some analyses. This data was for 54 fens on the Bohemian Massif and obtained from Hájek et al. (2014; see Electronic Appendix 1 for individual values). For three species (*Sarmentypnum exannulatum*, *Hamatocaulis vernicosus* and *Straminergon stramineum*) we had to use values obtained from neighbouring regions (see Electronic Appendix 1 for details). In Hájek et al. (2014) capitula of sphagna and apical segments of other moss species (length of about 2 cm) were sampled in 16 m^2 plots in the central parts of each fen. Moss samples were stored in polyethylene zip bags and refrigerated at 5 °C for up to 7 days prior to processing. Nitrogen and phosphorus concentrations in the moss biomass were determined by flow injection analysis (FIA) after digesting dried moss shoots in sulphuric acid (Kjeldahl digestion for ammonium determination as an indicator of organic nitrogen content) or in perchloric acid (for phosphorus). Potassium was determined by atomic absorption spectroscopy (AAS) after nitric acid digestion. For further details see Hájek et al. (2014) where these data were published.

Data analysis

To describe the ecological tolerances of the target species, we constructed box-and-whisker plots for the most frequent species in the historical and recent datasets. In order to consider differences in dominance, we used the original Braun-Blanquet cover codes to create three pseudospecies at the cut-off levels of 0, 1 and 25% of estimated relative cover. For each species, the hypothesized differences in the average pH in the two periods were tested using the t-test, while the hypothesized differences in pH variance were tested using the Brown-Forsythe test. The Brown-Forsythe test tests for equality of variances using medians and is used also for unbalanced datasets (i.e. different numbers of observations in the subsets compared) and for data with a skewed distribution (Brown & Forsythe 1974). These tests, however, did not include pseudospecies in order to avoid pseudoreplications. The Holm-Bonferroni correction was used to counteract the problem of multiple comparisons and a significance level $P < 0.05$ was used for this correction. This correction was done separately for the t- and Brown-Forsythe tests, respectively. In graphical presentation of box-and-whisker plots we refer to the corrected P-values.

Further, we quantified the magnitude of the change at the species level using the concept of species fidelity (Chytrý et al. 2002). We divided each dataset (both large and precise) into the two pH classes and calculated, for each species, its fidelity value (the phi-coefficient weighted by square-root of percentage species cover; Chytrý et al. 2002) to the groups of historical and recent plots. If the fidelity of a species to the group of recent relevés was higher than that to the group of historical relevés, we assigned a positive value to the phi-coefficient for the respective species. Conversely, if the fidelity of a species was higher to the group of historical relevés, we assigned a negative value to the phi-coefficient for the respective species. In the resulting table, we refer to this value as the ‘frequency × cover change’. In addition, we simply calculated the change in a species’ frequency between historical and recent relevés and referred to this value as the ‘frequency change’. We tested the significance of the frequency change using Fisher’s exact test. The frequency × cover change was not tested statistically, because Fisher's exact test cannot be calculated using abundances, and using pseudospecies would result in pseudoreplication. Finally, we plotted the species' frequency × cover change in the large dataset against the frequency × cover change in the precise dataset to determine the extent to which the results from both datasets correspond.

To test the hypothesis that the biomass of species that are increasing in abundance generally contain higher levels of nutrients than that of stable and declining species, we plotted the frequency × cover change value against recently recorded median concentrations of nitrogen, phosphorus and potassium in the biomass of each species recorded in the study region on the Bohemian Massif (data in Hájek et al. 2014). The regression relationships between the frequency × cover change of each species and the nutrient concentrations in their biomass were modelled for poor-fen and rich-fen subsets of both the large and precise datasets.

Results

Mean pH did not differ significantly (t-test; $P > 0.05$) between historical and recent relevés in both datasets (Fig. 2), but the pH variance in the large dataset differed significantly (Brown-Forsythe test; uncorrected $P = 0.004$). For the historical datasets the mean pH for the precise dataset was 5.22±0.82 and for the large dataset 5.38±0.71, and for recent datasets that for the precise dataset was 5.38±0.84 and for the large dataset 5.22±0.87.

Changes in species optima and variances in the precise dataset

In the precise dataset, *Bryum pseudotriquetrum* and *Scorpidium revolvens* agg. occurred recently under significantly (corrected $P < 0.05$) higher water pH (Fig. 3). Mean pH for *Campylium stellatum* agg. was also higher, but this effect was not significant after the Holm-Bonferroni correction (uncorrected $P = 0.032$). There was also a moderate but statistically insignificant shift of poor-fen species (*Polytrichum commune*, *Sphagnum fallax* and *S. palustre* agg.) to rich-fen conditions. In contrast, greater associations with low-pH conditions were rare and statistically insignificant. No change in the pH variance was significant in the precise dataset (Fig. 3, Table 1).

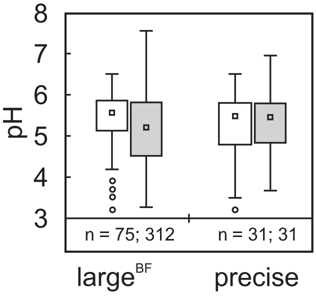


Fig. 2. – Comparison of the distribution of pH in records of historical (white boxes) and recent (grey boxes) vegetation plots, for both the large and precise datasets. Boxes indicate the 25–75% percentile, a small square within a box the median, whiskers the non-outlier range and small circles outliers and extremes. The superscript ^{BF} indicates statistically significant difference in variance between historical and recent datasets (Brown-Forsythe test); n = number of values.

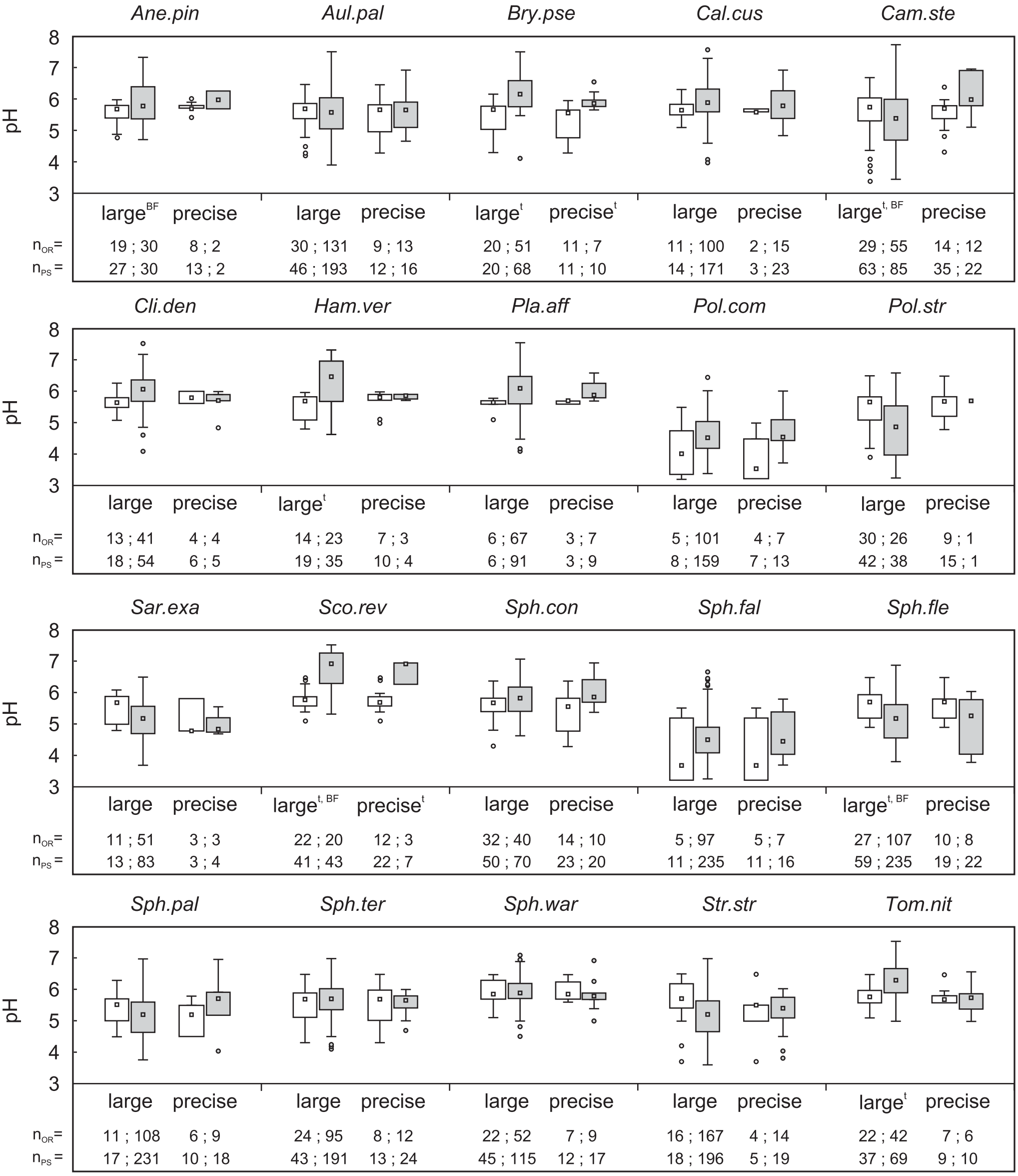


Fig. 3. – Distribution of pH values for particular species of fen bryophytes (including pseudospecies, see Materials and Methods) in historical (white boxes) and recent (grey boxes) vegetation plots in the large and precise datasets analysed separately. Boxes denote the 25–75% percentile. The small square within each box indicates the median. Whiskers indicate the non-outlier range, and small circles indicate outliers and extremes. The superscript ^{t} indicates statistically significant difference in means between the historical and recent datasets (t-test), and the superscript ^{BF} indicates statistically significant differences in variance between the historical and recent datasets (Brown-Forsythe test). Two numbers of replicates are presented (n ; n), the first refers to the original number of occurrences (used in statistical tests) and the second to the total number of values including pseudospecies (used in boxes). The significance level was $P < 0.05$, with the Holm-Bonferroni correction counteracting the problem of multiple comparisons. For abbreviations of bryophyte species names, see Table 1.

Table 1. – Alphabetically arranged list of the 20 most common species of bryophytes, their abbreviations used in the figures and the values of the change in frequency (Freq change) and change in frequency weighted by the square-root of a species' percentage cover (Freq × c change) in the two pH-classes. n = number of plots in which the species occurred in the historical (n_0) and recent (n_1) datasets, either in the large dataset (the first value) or the precise dataset (value in parenthesis). Change in frequency simply refers to a change in percentage frequency tested using Fischer's exact test (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

Species name	Abbrev.	Subset of poor-fens ($pH \leq 5$)						Subset of rich-fens ($pH > 5$)					
		Absolute frequency		Large dataset		Precise dataset		Absolute frequency		Large dataset		Precise dataset	
				Freq change	Freq × c change	Freq change	Freq × c change			Freq change	Freq × c change	Freq change	Freq × c change
		n_0	n_1	(%)	(phi)	(%)	(phi)	n_0	n_1	(%)	(phi)	(%)	(phi)
Aneura pinguis	Ane.pin	–	–	n. a.	n. a.	n. a.	n. a.	19 (8)	30 (2)	–14.09*	–0.067	–12.91*	–0.134
Aulacomnium palustre	Aul.pal	6 (3)	36 (2)	9.70	0.007	–4.14	–0.023	24 (6)	95 (11)	11.27	0.046	–4.35	0.023
Bryum pseudotriquetrum	Bry.pse	5 (4)	1 (–)	–8.21***	–0.132	–7.02	–0.156	15 (7)	50 (7)	1.77	0.030	–8.35	0.000
Calliergonella cuspidata	Cal.cus	–	8 (3)	4.49	0.068	1.69	0.161	11 (2)	92 (12)	32.39***	0.169	3.23**	0.226
Campylium stellatum agg.	Cam.ste	5 (3)	2 (–)	–7.65***	–0.162	–5.26	–0.178	24 (11)	53 (12)	–12.33	–0.172	–12.56	–0.201
Climacium dendroides	Cli.den	–	3 (1)	1.69	0.040	0.56	0.089	13 (4)	38 (3)	–1.46	–0.007	–5.33	0.002
Hamatocaulis vernicosus	Ham.ver	3 (1)	2 (–)	–4.14	–0.089	–1.75	–0.080	11 (6)	21 (3)	–7.50	–0.047	–8.84	–0.111
Plagiomnium affine agg.	Pla.aff	–	–	n. a.	n. a.	n. a.	n. a.	6 (3)	67 (7)	27.11***	0.120	–1.33	0.087
Polytrichum commune	Pol.com	4 (4)	74 (4)	34.56**	0.157	–4.77	0.091	1 (–)	27 (3)	13.41**	0.116	1.69	0.144
Polytrichum strictum	Pol.str	7 (2)	12 (–)	–5.54	–0.095	–3.51	–0.114	23 (7)	14 (1)	–32.49***	–0.157	–11.72*	–0.204
Sarmentypnum exannulatum	Sar.exa	4 (2)	20 (2)	4.22	0.005	–2.39	0.065	7 (1)	31 (1)	5.14	0.060	–1.19	–0.004
Scorpidium revolvens agg.	Sco.rev	–	–	n. a.	n. a.	n. a.	n. a.	22 (12)	20 (3)	–27.36***	–0.120	–19.37**	–0.168
Sphagnum contortum	Sph.con	4 (2)	4 (–)	–4.77**	–0.204	–3.51	–0.279	28 (12)	36 (10)	–28.90***	–0.093	–15.43	0.017
Sphagnum fallax	Sph.fal	3 (3)	72 (4)	35.19**	0.372	–3.02	0.230	2 (2)	25 (3)	10.54*	0.081	–1.82	–0.011
Sphagnum flexuosum	Sph.fle	1 (1)	41 (2)	21.28*	0.245	–0.63	0.183	26 (9)	66 (6)	–8.54	–0.055	–12.42	0.017
Sphagnum palustre agg.	Sph.pal	3 (2)	45 (1)	20.02	0.112	–2.95	–0.088	8 (4)	63 (8)	21.36**	0.182	–2.52	0.143
Sphagnum teres	Sph.ter	5 (3)	14 (2)	–0.91	–0.047	–4.14	0.077	19 (5)	81 (10)	12.17	0.091	–3.15	0.191
Sphagnum warnstorfii	Sph.war	–	3 (1)	1.69	0.059	0.56	0.099	22 (7)	49 (8)	–11.07	–0.030	–7.79	–0.001
Straminergon stramineum	Str.str	3 (2)	71 (3)	34.62**	0.134	–1.82	0.072	13 (2)	96 (11)	31.13***	0.101	2.67**	0.145
Tomentypnum nitens	Tom.nit	–	1 (1)	0.56	0.025	0.56	0.099	22 (7)	41 (5)	–15.56*	–0.059	–9.47	–0.046

Changes in species optima and variances in the large dataset

The results for pH means were similar when the large dataset was analysed, except for *Campylium stellatum* agg., which showed the opposite pattern. Statistically significant (corrected $P < 0.05$) associations with higher pH were recorded for *Hamatocaulis vernicosus*, *Bryum pseudotriquetrum*, *Scorpidium revolvens* agg. and *Tomentypnum nitens*. On the other hand, a significant shift of *S. flexuosum* to poor-fen conditions was recorded ($P = 0.001$). In the large dataset, pH variance was higher in the recent dataset than the historical dataset for eight species and for four of them (*Campylium stellatum* agg., *Scorpidium revolvens* agg., *Sphagnum flexuosum*, *Aneura pinguis*) the difference remained statistically significant after the Holm-Bonferroni correction (Fig. 3).

Changes in cover and frequency of bryophytes in poor fens

The frequency × cover changes recorded for particular species in the large and precise datasets (Table 1) were significantly highly correlated ($P < 0.01$; Fig. 4) within both the poor-fen and rich-fen subset, indicating that the rough database data yielded similar results to the more precise yet smaller subset. The correlation was stronger for the rich-fen subset ($r^2 = 0.79$ vs 0.69). In general terms, the results were similar when the large and precise dataset were used, with few exceptions.

Using the frequency × cover changes recorded in poor fens ($pH \leq 5$), there was an increase in abundance of *Sphagnum fallax* and *S. flexuosum* in both large and precise datasets, and an increase of abundance of *Calliergonella cuspidata* in the precise dataset. On the other hand abundance of *S. contortum* (the most clearly), *Campylium stellatum*, *Bryum pseudotriquetrum*, *Hamatocaulis vernicosus* and *Polytrichum strictum* decreased. Inconsistent directions of the frequency × cover changes were recorded for *S. teres* and *S. palustre*, but for poor fens there was very little change recorded for both of these species.

Changes in cover and frequency in rich fens

Using the frequency × cover changes recorded in rich fens, the abundance of *Calliergonella cuspidata*, *S. teres* (more clearly in the precise dataset), *Sphagnum palustre* agg., *Straminergon stramineum*, *Polytrichum commune* and *Plagiomnium affine* agg. increased, while abundance of *Campylium stellatum* agg., *Polytrichum strictum*, *Scorpidium revolvens* agg., *Aneura pinguis* and *Hamatocaulis vernicosus* decreased (Fig. 5). Other species were either stable, or displayed inconsistent changes in the two datasets.

When cover was not considered, two other species that changed in frequency of occurrence in rich fens were identified: *Straminergon stramineum* increased in frequency and *Sphagnum contortum* decreased (Table 1).

Relationship between the intensity of species dynamics and concentrations of nutrients in their tissues

In rich fens ($pH > 5$), the change in the frequency × cover for particular species linearly positively correlated with recent records of the concentrations of nitrogen, potassium and phosphorus in their tissues (Fig. 5). In the case of the large dataset, we found significant results ($P < 0.05$) for all three nutrients analysed, most notably for potassium ($r^2 = 0.23$, $P = 0.01$). In the case of the precise dataset, changes in the frequency × cover were only significantly correlated with potassium ($r^2 = 0.23$, $P = 0.04$), but not nitrogen ($r^2 = 0.10$, $P = 0.1$) or phosphorus ($r^2 = 0.15$, $P = 0.103$).

In the subset of fens with a pH lower than 5, there was no relationship between the intensity of species dynamics and the nutrient concentrations in their tissues.

Discussion

Changes in species tolerances and frequencies

We found that calcicole brown mosses now occur only in the most alkaline fen patches. The same species have also declined in Dutch fens (Kooijman et al. 1994, Paulissen et al. 2014). The substantial decline in brown mosses, which is not balanced out by a similar increase in some other species, indicates that brown mosses are being outcompeted around the centre of the pH/calcium gradient by species that are not extending their pH niche, but merely profiting from ongoing environmental changes, especially eutrophication. Nevertheless, other effects of these changes, such as ammonium toxicity (Paulissen et al. 2005, Kooijman & Paulissen 2006), occasional drought or increasing shading by vascular plants may also contribute to the decline in brown mosses.

Analysis of the frequency × cover change in the precise dataset revealed that *Calliergonella cuspidata*, *Sphagnum palustre* agg. and *S. teres* are the species that are most likely to threaten other species of fen bryophytes. Together with the increasing frequency of *Straminergon stramineum*, this may indicate the beginning of a deterioration in natural fen habitats. This is supported by the increase in abundance of these species recorded in permanent plots in the Třeboň basin (J. Navrátilová, personal observations). These permanent plots, however, are yet to be thoroughly resampled. Because these species are a natural component of fen habitats and because they are morphologically very similar to other fen bryophytes, nature conservancy authorities may not be able to record this change in vegetation. The frequent co-occurrence of *C. cuspidata*, *S. teres* and *H. vernicosus* recorded on the Bohemian Massif and in Bulgaria (Štechová et al. 2008), thus represent a serious threat to the European endangered species *H. vernicosus*.

The same species are recorded increasing in cover in fens worldwide. Bursik & Moseley (1992) record an expansion of *S. teres*, *S. centrale* (*S. palustre* agg.) and *Straminergon stramineum* in one Idahoan fen (USA). *Calliergonella cuspidata* (Kooijman 2012) and *Sphagnum palustre* (Paulissen et al. 2014) are recognized as some of the species that threaten specialist bryophyte species in fens in the Netherlands. In the case of *C. cuspidata*, our analysis matches experimental results and empirical knowledge better than a simple comparison of the frequencies in phytosociological data from the Dutch database (Paulissen et al. 2014), which indicate a decline in the abundance of this species. The increase in the abundance of *S. teres* has not yet been explicitly addressed in Europe, but its allied species *Sphagnum squarrosum* is increasing in eutrophicated fens in the Netherlands (Kooijman 2012).

Niche contraction or extinction of a previously undiscovered species?

The fact that both *S. revolvens* agg. and *C. stellatum* agg. consist of previously undistinguished taxa may have some bearing on the interpretation of the conspicuously changing

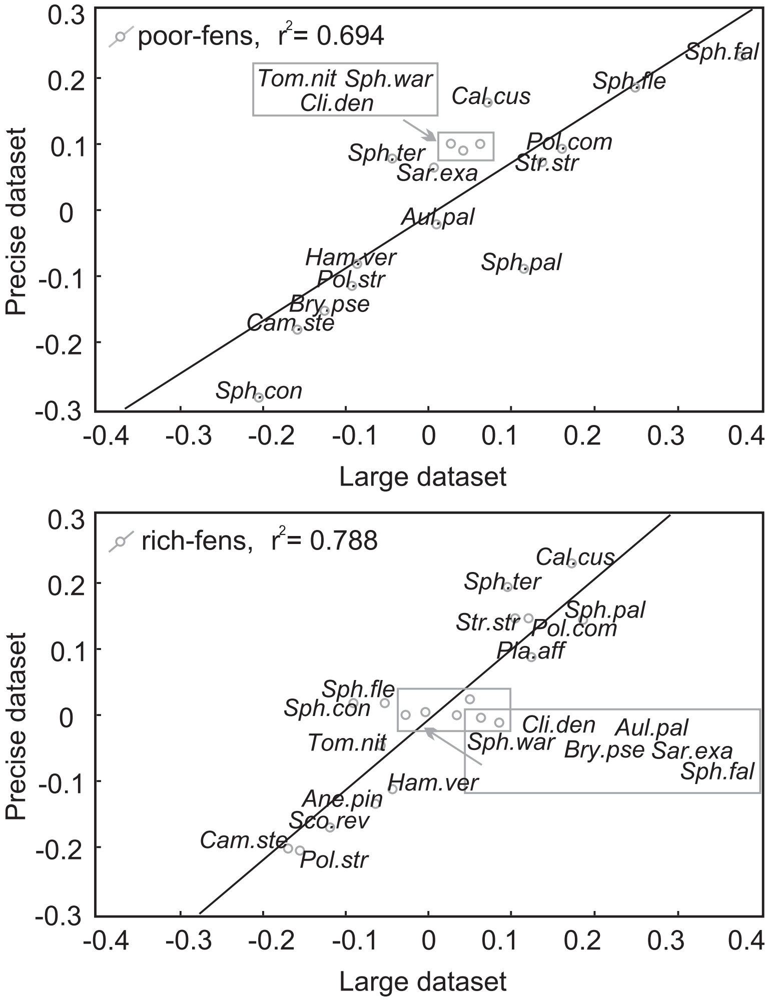
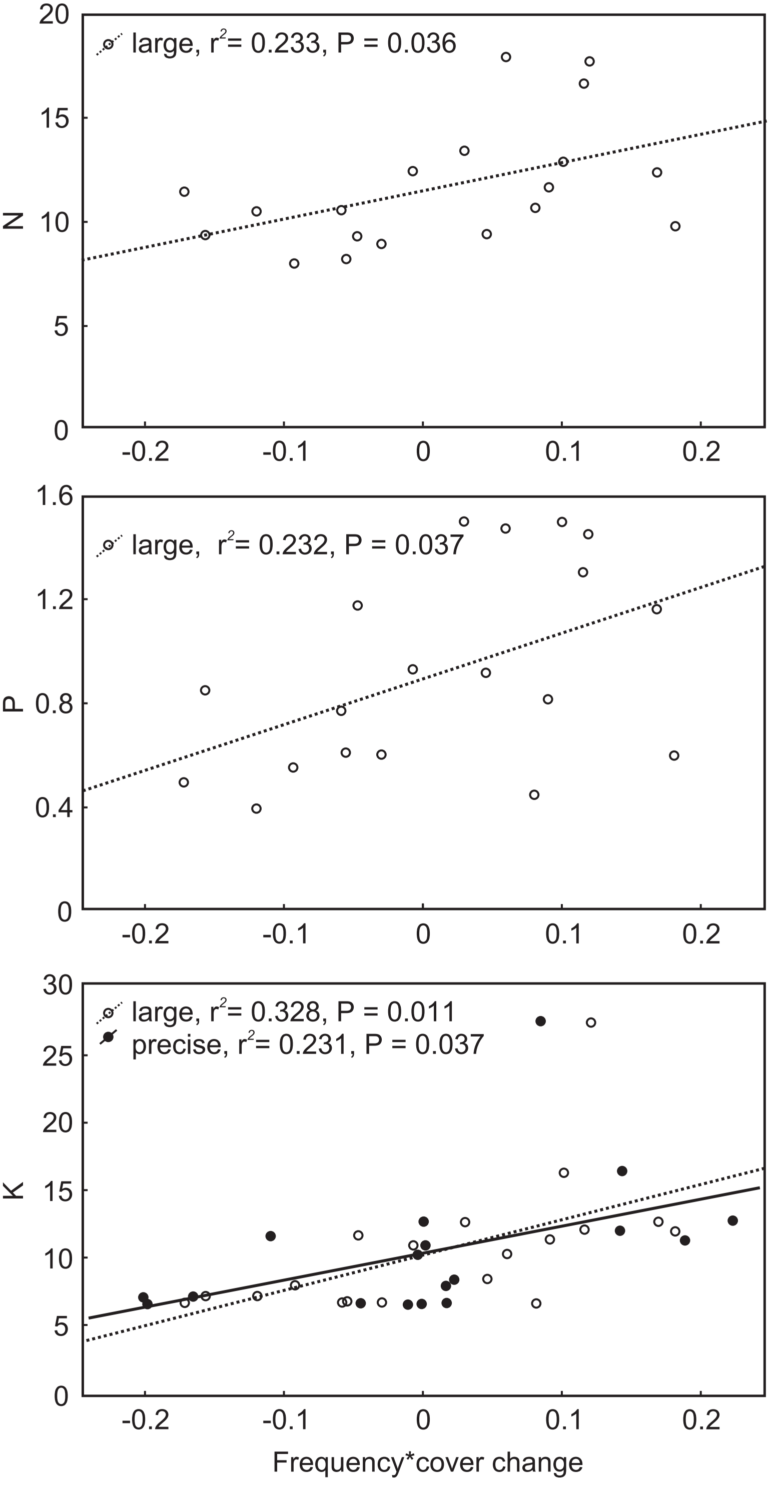


Fig. 4. – Comparison of the frequency × cover change of the analysed species in the large and precise datasets for the two pH classes (poor-fens = pH 3–5; rich-fens = pH 5–8). Positive values indicate higher abundance in recent vegetation plots, and negative values a higher abundance in historical vegetation plots. For abbreviations of bryophyte species names, see Table 1.

Fig. 5. – Relationship between the frequency × cover change of the analysed species of bryophytes in rich fens (pH > 5) and the recent median concentrations of nutrient (N = nitrogen, P = phosphorus, K = potassium) in their biomass (in mg·g^{-1} dry mass) recorded across the entire study area (see Electronic Appendix 1 for details). Each point represents one species. Only statistically significant relationships are presented (unadjusted $P < 0.05$). For potassium, both datasets yielded statistically significant relationships, which are presented in a single scatter. Note that the restriction of the analysis to 15 species with the highest absolute value of the frequency × cover change would strengthen the relationship for potassium in the precise dataset ($r^2 = 0.35$, $P = 0.026$).

▶▶▶


large, r^2= 0.233, P = 0.036
N
20
15
10
5
0
-0.2
-0.1
0
0.1
0.2
large, r^2= 0.232, P = 0.037
P
1.6
1.2
0.8
0.4
0
-0.2
-0.1
0
0.1
0.2
large, r^2= 0.328, P = 0.011
precise, r^2= 0.231, P = 0.037
K
30
25
20
15
10
5
0
-0.2
-0.1
0
0.1
0.2
Frequency*cover change

ecological behaviour of these aggregates. The *S. revolvens* aggregate includes two species, *S. revolvens* s.s and *S. cossonii*. The former prefers less alkaline and less calcium-rich habitats, and occurs in fens with a pH of about 5.0–5.5 and conductivity of about 50 $\mu S.cm^{-1}$ (Kooijman & Hedenäs 1991, Tahvanainen 2004), which according to our dataset is the same environment from which the *S. revolvens* agg. has disappeared. *Scorpidium revolvens* s.s. seems to be rare in the Czech Republic (Kučera 2005), but we cannot rule out that historical plots contained both species and that *S. revolvens* s.s. recently became extremely rare or even became extinct in the study area. Similarly, two species, *C. stellatum* and *C. protensum*, were recently recognized within the *C. stellatum* agg. (compare Hedenäs 2003). Differences in their ecological requirements have yet to be determined, but one cannot exclude a similar scenario to that proposed above for *S. revolvens*. The existence of these two alternative explanations, however, does not cast doubt on our main conclusion that specialized fen bryophytes are decreasing whereas the more nutrient-demanding or ubiquitous species are increasing.

On the other hand, the ability to distinguish between species in the *S. recurvum* complex is a unique property of our datasets. In phytosociological databases, these species are usually merged (Paulissen et al. 2014). Our analysis revealed slightly different behaviour in these closely related, but genetically distinct (Szurdoki et al. 2014) species. *Sphagnum flexuosum* was the only species in our analysis for which the recent pH median was significantly lower and pH variance higher. This result, along with the results for the frequency × cover change, indicates it has greatly increased in poor fens whereas some other peat mosses, *S. contortum*, *S. subsecundum* and *S. magellanicum* (Table in Electronic Appendix 1), have decreased. *Sphagnum fallax* has also increased in poor fens, but because this species previously frequently occurred in poor fens, the change is not as conspicuous as in the case of *S. flexuosum*. As regards changes in the frequency and frequency × cover of *S. fallax*, this species increased significantly in high-pH fens in the large dataset, unlike *S. flexuosum*, but this was not confirmed by the analysis of the precise dataset. Thus, we found little support for the initial hypothesis of Hájek et al. (2002) and Navrátilová et al. (2006) that the increase in *S. fallax/flexuosum* in rich fens is one of the major reasons why rich fens are becoming rarer in the study area. These species increase more in poor than rich fens, and pose a threat to low-productive, waterlogged, moderately-rich fens with *Rhynchospora alba* and *Sphagnum* sect. *Subsecunda* and poor fens with *S. magellanicum*. Both these vegetation types are slowly disappearing from the study area (Navrátilová & Navrátil 2005b, Hájek & Hájková 2011). Limpens et al. (2003) confirm experimentally that the increase of *S. fallax* in acidic mires is triggered by an increase in the availability of nitrogen and phosphorus.

Causal processes that drive the observed changes

We demonstrate that fen species that are increasing in the study area generally have higher concentrations of nutrients in their tissues, especially potassium, than stable and declining species. The fact that rich-fen specialists survive mainly in high-pH (usually calcium-rich) conditions may also coincide with nutrient availability: high calcium supply generally decreases nutrient (especially phosphorus) availability (Boyer & Wheeler 1989, Kooijman & Hedenäs 2009).

High potassium concentration in tissues is a trait that coincides with species' ability to replace other species in succession. Potassium regulates osmosis and turgor pressure, and an enhanced concentration may be necessary for fast-growing plant species; fast-growing broad-leaved vascular plants that occur in advanced stages of fen succession also have enhanced concentration of potassium in their tissues (Rozbrojová & Hájek 2010). Enhanced potassium availability further helps these fast growing, competitively strong, species to utilize more effectively light for photosynthesis as there is increasing evidence that improving potassium nutritional status can greatly lower light-induced oxidative stress and hence maintain photosynthetic electron transport (Cakmak 2005).

Calliergonella cuspidata and *S. teres* are the species with the highest concentration of potassium in the study area (Hájek et al. 2014). Both these species as well as other species with high biomass potassium concentrations grow not only in sedge-moss fens, but also in wet broadleaved grass-rich grasslands (the *Calthion* alliance). Their high potassium concentrations may not only coincide with high nutrient demands, but may also benefit moss species growing in habitats with fluctuating water table, because desiccation usually leads to potassium loss through damaged cytoplasmic membranes (Brown & Buck 1979). This fact somewhat challenges the tempting interpretation of the recorded changes in terms of nutrient enrichment in agricultural landscapes. Even though most of the fens studied were not drained, wide-scale landscape transformations may have so altered hydrological processes that even undrained fens may be affected (Bedford 1996). We are therefore facing a similar question as authors that revisited mires in Scandinavia (Gunnarsson et al. 2000, Kapfer et al. 2011) and Switzerland (Bollens et al. 2001, Moradi et al. 2012): How to disentangle the effects of eutrophication and lowering of the water table?

Unfortunately, our data cannot unequivocally answer this question, although it does contain certain indices. The abundance of *Calliergonella cuspidata* has increased in eutrophicated fens (see also Kooijman 2012), but laboratory experiments suggest that it does not benefit from nutrient enrichment more than threatened fen brown mosses (Kooijman & Paulissen 2006, Vicherová et al. 2015). It could, however, have benefited from the slight increase in shading provided by the herbaceous plant layer the biomass of which increases with eutrophication (Bergamini & Peintinger 2002). Nevertheless, dynamics of other species indicate nutrient enrichment rather than a lowering of the water table. Remarkably, *Straminergon stramineum* increased in frequency. Its frequency has also increased in permanent plots located in Czech ombrotrophic bogs exposed to high aerial nitrogen deposition (Hájková et al. 2011a). In addition, its ecological optimum is in acidic fens with increased net N mineralization (Kooijman & Hedenäs 2009). Concerning water demand, this species may grow semi-aquatically in poor, floating fens early in a hydrosere (Bursik & Moseley 1992, Swinehart & Parker 2000). In addition, our results also indicate that certain other semi-aquatic mosses, such as *Sarmentypnum exannulatum* and *Sphagnum denticulatum*, have not declined in abundance, but the hummock-dwelling species *Polytrichum strictum* has. *Polytrichum commune,* another hummock-forming but larger and more nutrient-demanding species, has increased. There was no statistically significant shift of *Sphagnum warnstorfii* to more calcareous conditions, which would indicate a lowering of the water table (Granath et al. 2010, Hájek et al. 2014). All these facts indicate that the recorded changes are caused more probably by nutrient enrichment than a lowering of the water table. This conclusion is in line not only with increasing nitrogen deposition in central Europe (Jiroušek et al. 2011), but also with heavy fertilization of arable land and productive hay meadows (Růžička 1989) as well as fertilization of fishponds with fens at their margins (Pechar et al. 2002).

Our data indicate an important role of potassium in fen succession. On the Bohemian Massif the groundwater potassium levels are naturally high because of weathering feldspars in the bedrock (Peterka et al. 2014), but increased in 1970–1980s, when there was a great increase in the application of fertilizers to arable land. Majer et al. (2012) report higher potassium concentrations in the period 1984–1996 than more recently (2007–2010). The potassium accumulation in fens on the Bohemian Massif could be further supported by lack of traditional mowing of most fens between 1980–1990s, because mowing usually removes potassium from wetland ecosystems (Olde Venterink et al. 2003).

Cusell et al. (2014) report that nutrients coming from heavily fertilized surroundings are filtered by vegetation at the periphery of wetlands. In the case of small fen remnants, this is not the case, so nutrients directly affect their most valuable central parts. Even a low nutrient input, provided that it is long-term, may gradually alter fen communities and turn them into depauperate, grassland-like wetlands with a prevalence of generalists over habitat specialists. The ultimate aims of nature conservancy authorities should therefore be to prevent nutrient input into fens, for example, by creating protected nutritional and hydrological buffer zones, to maintain nutrient export via mowing and hay removal, and, naturally, to thoroughly monitor any changes that take place in the bryophyte layer of seemingly well preserved fens.

Conclusion

We compared the records of historical and recent vegetation plots from seemingly untouched fens on the Bohemian Massif (central Europe). We hypothesized (i) an increase in tolerance of acidicolous peat mosses to pH during the last half century and (ii) increase in abundance of fast-growing species with high tissue nutrient concentrations. For the most dynamic species, our analysis yielded the same conclusions for both the precise (small but less biased) dataset, compensated for spatial mismatch between old and new plots, and the large but spatially unbalanced dataset, compensated for a low number of replicates (but see contrasting result for *Campylium stellatum*, Fig. 3). The first hypothesis was confirmed only partially as the competitively strong poor-fen species (including *S. fallax* and *S. flexuosum*) did not increase in abundance in rich fens and only conspicuously increased in poor fens. *Sphagnum palustre* agg. and *S. teres* increased in abundance in rich fens, indicating an increased pH tolerance, but their pH optima and amplitudes did not differ from those recorded in the past.

A more clear result was that brown mosses specialized for growing in fens (*Scorpidium revolvens* agg., *Bryum pseudotriquetrum*, *Tomentypnum nites*, *Hamatocaulis vernicosus*) are gradually being replaced by more nutrient-demanding species, namely *Calliergonella cuspidata*, *Sphagnum palustre* agg., *S. teres* and *Straminergon stramineum*, in rich fens, and are currently mainly found in the most alkaline conditions. Increasing species were those with a high tissue potassium concentration, which corroborates the second hypothesis. At first glance, these changes may seem subtle, because the increasing species are natural components of fen vegetation and may belong to the same functional groups or even the same genera as decreasing species. Nature conservationists, who are usually not trained in bryophyte identification, may therefore overlook these early signs of fen eutrophication that may end in complete transformation of a pristine fen into another, grassland- or reed-like habitat. Changes in the species composition of the moss layer should therefore be closely monitored, and if an increase in nutrient-demanding species of mosses are detected, countermeasures should be applied.

See www.preslia.cz for Electronic Appendix 1

Acknowledgements

This paper is dedicated to the memory of Kamil Rybníček (1933–2014) who thoroughly studied fen vegetation in the study region and who taught us to understand its ecology. He also helped us find historical locations of vegetation plots. We further thank all colleagues that helped during field sampling, especially Daniel Dítě. Our kind colleagues Eliška Vicherová and Eva Mikulášková are acknowledged for identifying or revising certain critical bryophyte specimens and providing unpublished data. Fred Rooks helped out with our English and Tony Dixon edited the accepted version of the paper. Ondřej Hájek created the map. Táňa Štechová, Filip Lysák, Adam Veleba and Petr Bureš shared our enthusiasm for the fascinating ecosystem of rich fens on this part of the Bohemian Massif. This research was supported by the Czech Science Foundation (grant number P505/10/0638) and the long-term research development project of the Institute of Botany, The Czech Academy of Sciences (RVO 67985939).

Souhrn

Ze slatinišť temperátní zóny se v současnosti rychle ztrácí specializované druhy. To se děje i na slatiništích, která se zdánlivě jeví jako nedotčená, avšak probíhá na nich rychlá sukcese v mechovém patře. V České republice podobný vývoj pozorujeme také, avšak přímé srovnání historických a současných vegetačních dat nebylo dosud provedeno. V tomto článku jsme analyzovali historický soubor fytocenologických snímků z Třeboňska a Českomoravské vrchoviny, zapsaných K. Rybníčkem a P. Březinou před 45–65 lety, a recentní datový soubor, získaný po roce 2000. Testovali jsme hypotézu, která vyplynula z předchozího výzkumu vztahů mezi recentní vegetací a chemismem prostředí, že kyselomilné a kompetičně silné živinově náročnější druhy mechorostů v území expandují a rozšiřují svoji toleranci k bazickým podmínkám. Pracovali jsme se dvěma datovými soubory: velkým, pokrývajícím dostatek snímků z celého území, a menším podsouborem, zahrnujícím pouze floristicky nejpodobnější snímky ze stejných lokalit, které byly zkoumány v minulosti i v současnosti. Zjistili jsme, že vápnomilné slatiništní mechy přežily do současnosti jen na nejbazičtějších místech. Z méně extrémních míst byly vytlačeny kompetičně zdatnějšími, avšak živinově náročnějšími druhy *Calliergonella cuspidata*, *Sphagnum palustre*, *S. teres* a *Straminergon stramineum*. Kyselomilné rašeliníky *Sphagnum fallax* a *S. flexuosum* expandovaly jen na přechodových rašeliništích a nikoliv na vápnitějších typech slatinišť, jak jsme původně předpokládali. Pro analyzované druhy mechů jsme měli díky předchozí studii k dispozici jejich mediánovou koncentraci draslíku, fosforu a dusíku v biomase ve studovaném území. Tuto proměnnou jsme korelovali s mírou pozorované změny v abundanci druhu a zjistili, že ve slatiništích expandují druhy s velkou koncentrací živin, zejména draslíku. Expanze těchto druhů zůstává často dlouho nepovšimnuta, i když může signalizovat časné fáze eutrofizace biotopu, protože ochránci přírody ne vždy jednotlivé druhy mechů rozlišují. Poslední zbytky slatinišť v naší zemědělské krajině tedy vyžadují pravidelný monitoring mechového patra, aby bylo možné včas provést případná opatření proti postupující eutrofizaci.

References

Bedford B. L. (1996): The need to define hydrologic equivalence at the landscape scale for freshwater wetland mitigation. – Ecol. Appl. 6: 57–68.

Bergamini A. & Peintinger M. (2002): Effects of light and nitrogen on morphological plasticity of the moss *Calliergonella cuspidata*. – Oikos 96: 355–363.

Bergamini A., Peintinger M., Fakheran S., Moradi H., Schmid B. & Joshi J. (2009): Loss of habitat specialists despite conservation management in fen remnants 1995–2006. – Persp. Plant Ecol. Evol. Syst. 11: 65–79.

Bollens U., Güsewell S. & Klotzli F. (2001): Vegetation changes in two Swiss fens affected by eutrophication and desiccation. – Bot. Helv. 111: 121–137.

Boyer M. L. H. & Wheeler B. D. (1989): Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. – J. Ecol. 77: 597–609.

Březina P., Hadač E., Ježek V. & Kubička J. (1963): Poznámky o vegetaci Třeboňských blat [Notes on vegetation of Třeboň mires]. – Sborn. Pedag. Inst. Plzeň, Zeměpis a přírodopis 4: 207–272.

Brown D. H. & Buck G. W. (1979): Desiccation effects and cation distribution in bryophytes. – New Phytol. 82: 115–125.

Brown M. B. & Forsythe A. B. (1974): Robust tests for equality of variances. – J. Am. Stat. Assoc. 69: 364–367.

Bursik R. J. & Moseley R. K. (1992): Forty-year changes in Hager Lake Fen, Bonner County, Idaho. – Idaho Department of Fish and Game, Conservation Data Center, Boise
URL: http://fishandgame.idaho.gov/ifwis/idnhp/cdc_pdf/bursr92c.pdf (accessed 12 March 2015).

Butchart S. H., Walpole M., Collen B., van Strien A., Scharlemann J. P., Almond R. E. A., Baillie J. E. M., Bomhard B., Brown C., Bruno J., Carpenter K. E., Carr G. M., Chanson J., Chenery A. M., Csirke J., Davidson N. C., Dentener F., Foster M., Galli A., Galloway J. N., Genovesi P., Gregory R. D., Hockings M., Kapos V., Lamarque J.-F., Leverington F., Loh J., McGeoch M. A., McRae L., Minasyan A., Hernández Morcillo M., Oldfield T. E. E., Pauly D., Quader S., Revenga C., Sauer J. R., Skolnik B., Spear D., Stanwell-Smith D., Stuart S. N., Symes A., Tierney M., Tyrrell T. D., Vié J.-C. & Watson R. (2010): Global biodiversity: indicators of recent declines. – Science 328: 1164–1168.

Cakmak I. (2005): The role of potassium in alleviating detrimental effects of abiotic stresses in plants. – J. Plant. Nutr. Soil. Sci. 168: 521–530.

Chytrý M., Tichý L., Hennekens S. M. & Schaminée J. H. J. (2014): Assessing vegetation change using vegetation-plot databases: a risky business. – Appl. Veg. Sci. 17: 32–41.

Chytrý M., Tichý L., Holt J. & Botta-Dukát Z. (2002): Determination of diagnostic species with statistical fidelity measures. – J. Veg. Sci. 13: 79–90.

Colombaroli D. & Tinner W. (2013): Determining the long-term changes in biodiversity and provisioning services along a transect from Central Europe to the Mediterranean. – Holocene 23: 1625–1634.

Cusell C., Kooijman A., Fernandez F., van Wirdum G., Geurts J. J., van Loon E. E., Kalbitz K. & Lamers L. P. M. (2014): Filtering fens: mechanisms explaining phosphorus-limited hotspots of biodiversity in wetlands adjacent to heavily fertilized areas. – Sci. Total Environ. 481: 129–141.

Cusell C., Lamers L. P. M., van Wirdum G. & Kooijman A. (2013): Impacts of water level fluctuation on mesotrophic rich fens: acidification vs. eutrophication. – J. Appl. Ecol. 50: 998–1009.

Danihelka J., Chrtek J. Jr. & Kaplan Z. (2012): Checklist of vascular plants of the Czech Republic. – Preslia 84: 647–811.

Diemer M., Oetiker K. & Billeter R. (2001): Abandonment alters community composition and canopy structure of Swiss calcareous fens. – Appl. Veg. Sci. 4: 237–246.

Dullinger S., Essl F., Rabitsch W., Erb K. H., Gingrich S., Haberl H., Hülber K., Jarošík V., Krausmann F., Kühn I., Pergl J., Pyšek P. & Hulme P. E. (2013): Europe's other debt crisis caused by the long legacy of future extinctions. – Proc. Natl. Acad. Sci. U.S.A. 110: 7342–7347.

du Rietz G. E. (1949): Huvudenheter och huvudgränser i svensk myrvegetation [Main units and main limits in Swedish mire vegetation]. – Svensk Bot. Tidskr. 43: 279–304.

Essl F., Dullinger S., Moser D., Rabitsch W. & Kleinbauer I. (2012): Vulnerability of mires under climate change: implications for nature conservation and climate change adaptation. – Biodiv. Cons. 21: 655–669.

Feurdean A., Willis K. J., Parr C. L., Tanţău I. & Fărcaş S. (2010): Post-glacial patterns in vegetation dynamics in Romania: homogenization or differentiation? – J. Biogeogr. 37: 2197–2208.

Fojt W. & Harding M. (1995): Thirty years of change in the vegetation communities of three valley mires in Suffolk, England. – J. Appl. Ecol. 32: 561–577.

Graf U., Wildi O., Küchler M. & Ecker K (2010): Five-year changes in Swiss mire vegetation. – Bot. Helv. 120: 15–27.

Granath G., Strengbom J. & Rydin H. (2010): Rapid ecosystem shifts in peatlands: linking plant physiology and succession. – Ecology 91: 3047–3056.

Grootjans A. P., Hunneman H., Verkiel H. & van Andel J. (2005): Long-term effects of drainage on species richness of a fen meadow at different spatial scales. – Basic Appl. Ecol. 6: 185–193.

Gunnarsson U., Rydin H. & Sjörs H. (2000): Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, Central Sweden. – J. Veg. Sci. 11: 277–286.

Hájek M. & Hájková P. (2011): Vegetace slatinišť, přechodových rašelinišť a vrchovištních šlenku (*Scheuchzerio palustris-Caricetea nigrae*) [Vegetation of fens, transitional mires and bog hollows]. – In: Chytrý M. (ed.), Vegetace České republiky 3. Vodní a mokřadní vegetace [Vegetation of the Czech Republic 3. Aquatic and wetland vegetation], p. 614–704, Academia, Praha.

Hájek M. & Hekera P. (2004): Can seasonal variation in fen water chemistry influence the reliability of vegetation-environment analyses? – Preslia 76: 1–14.

Hájek M., Hekera P. & Hájková P. (2002): Spring fen vegetation and water chemistry in the Western Carpathian flysch zone. – Folia Geobot. 37: 205–224.

Hájek M., Plesková Z., Syrovátka V., Peterka T., Laburdová J., Kintrová K., Jiroušek M. & Hájek T. (2014): Patterns in moss element concentrations in fens across species, habitats, and regions. – Persp. Plant Ecol. Evol. Syst. 16: 203–218.

Hájková P., Hájek M., Rybníček K., Jiroušek M., Tichý L., Králová Š. & Mikulášková E. (2011a): Long-term vegetation changes in bogs exposed to high atmospheric deposition, aerial liming and climate fluctuation. – J. Veg. Sci. 22: 891–904.

Hájková P., Horsák M., Hájek M., Lacina A., Buchtová H. & Pelánková B. (2012): Origin and contrasting succession pathways of the Western Carpathian calcareous fens revealed by plant and mollusc macrofossils. – Boreas 41: 690–706.

Hájková P., Jamrichová E., Horsák M. & Hájek M. (2013): Holocene history of a *Cladium mariscus*-dominated calcareous fen in Slovakia: vegetation stability and landscape development. – Preslia 85: 289–315.

Hájková P., Roleček J., Hájek M., Horsák M., Fajmon K., Polák M. & Jamrichová E. (2011b): Prehistoric origin of extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts. – Preslia 83: 185–204.

Hedenäs L. (2003): The European species of the *Calliergon-Scorpidium-Drepanocladus* complex, including some related or similar species. – Meylania 28: 1–116.

Hédl R. (2004): Vegetation of beech forests in the Rychlebské Mountains, Czech Republic, re-inspected after 60 years with assessment of environmental changes. – Plant Ecol. 170: 243–265.

Heino J., Virtanen R., Vuori K. M., Saastamoinen J., Ohtonen A. & Muotka T. (2005): Spring bryophytes in forested landscapes: land use effects on bryophyte species richness, community structure and persistence. – Biol. Cons. 124: 539–545.

Horodyská E. (2006): Minerotrofní rašeliniště Českomoravské vrchoviny: srovnání historických a současných dat [Minerotrophic mires of Bohemian-Moravian Uplands: comparisson of historical and contemporary data]. – Master thesis, Department of Botany and Zoology, Masaryk University, Brno, URL: http://is.muni.cz/th/52491/prif_m/zacatek.pdf.

Jamrichová E., Hájková P., Horsák M., Rybníčková E., Lacina A. & Hájek M. (2014): Landscape history, calcareous fen development and historical events in the Slovak Eastern Carpathians. – Veg. Hist. Archaeobot. 23: 497–513.

Jensen K. & Schrautzer J. (1999): Consequences of abandonment for a regional fen flora and mechanisms of successional change. – Appl. Veg. Sci. 2: 79–88.

Jiroušek M., Hájek M. & Bragazza L. (2011): Nutrient stoichiometry in *Sphagnum* along a nitrogen deposition gradient in highly polluted region of Central-East Europe. – Environ. Pollut. 159: 585–590.

Jiroušek M., Poulíčková A., Kintrová K., Opravilová V., Hájková P., Rybníček K., Kočí M., Bergová K., Hnilica R., Mikulášková E., Králová Š. & Hájek M. (2013): Long-term and contemporary environmental conditions as determinants of the species composition of bog organisms. – Freshw. Biol. 58: 2196–2207.

Juutinen R. (2011): The decrease of rich fen bryophytes in springs as a consequence of large-scale environmental loss: a 50-year re-sampling study. – Lindbergia 34: 2–18.

Kapfer J., Grytnes J.-A., Gunnarsson U. & Birks H. J. B. (2011): Fine-scale changes in vegetation composition in a boreal mire over 50 years. – J. Ecol. 99: 1179–1189.

Koch M. & Jurasinski G. (2014): Four decades of vegetation development in a percolation mire complex following intensive drainage and abandonment. – Plant Ecol. Divers. 8: 49–60.

Kooijman A. M. (2012): ‘Poor rich fen mosses’: atmospheric N-deposition and P-eutrophication in base-rich fens. – Lindbergia 35: 42–52.

Kooijman A. M., Beltman B. & Westhoff V. (1994): Extinction and reintroduction of the bryophyte *Scorpidium scorpioides* in a rich-fen spring site in the Netherlands. – Biol. Cons. 69: 87–96.

Kooijman A. M. & Hedenäs L. (1991): Differentiation in habitat requirements within the genus *Scorpidium*, especially between *S. revolvens* and *S. cossonii*. – J. Bryol. 16: 619–627.

Kooijman A. M. & Hedenäs L. (2009): Changes in nutrient availability from calcareous to acid wetland habitats with closely related brown moss species: increase instead of decrease in N and P. – Plant Soil 324: 267–278.

Kooijman A. M. & Kanne D. M. (1993): Effects of water chemistry, nutrient supply and interspecific interactions on the replacement of *Sphagnum subnitens* by *S. fallax* in fens. – J. Bryol. 17: 431–438.

Kooijman A. M. & Paulissen M. P. C. P. (2006): Higher acidification rates in fens with phosphorus enrichment. – Appl. Veg. Sci. 9: 205–212.

Kopecký M. & Macek M. (2015): Vegetation resurvey is robust to plot location uncertainty. – Divers. Distrib. 21: 322–330.

Kučera J. (2005): Zajímavé bryofloristické nálezy [Interesting bryofloristic records] VI. – Bryonora 36: 26–34.

Kučera J., Váňa J. & Hradílek Z. (2012): Bryophyte flora of the Czech Republic: updated checklist and Red List and a brief analysis. – Preslia 84: 813–850.

Küchler H., Grünig A., Hangartner R. & Küchler M. (2009): Vegetation change and effects of cattle grazing in the transition mire "Burgmoos". – Bot. Helv. 119: 95–104.

Lamers L. P. M., Vile M. A., Grootjans A. P., Acreman M. C., van Diggelen R., Evans M. G., Richardson C. J., Rochefort L., Kooijman A. M., Roelofs J. G. M. & Smolders A. J. P. (2015): Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. – Biol. Rev. 90: 182–203.

Limpens J., Tomassen H. B. & Berendse F. (2003): Expansion of *Sphagnum fallax* in bogs: striking the balance between N and P availability. – J. Bryol. 25: 83–90.

Majer V., Hruška J., Zoulková V., Holečková P. & Myška O. (2012): Atlas chemismu povrchových vod České republiky, stav v letech 1984–1996 a 2007–2010 [Atlas of chemistry of surface waters of the Czech Republic, the state in years 1984–1996 and 2007–2010]. – Česká geologická služba, Praha.

Mälson K., Backéus I. & Rydin H. (2008): Long-term effects of drainage and initial effects of hydrological restoration on rich fen vegetation. – Appl. Veg. Sci. 11: 99–106.

Moradi H., Fakheran S., Peintinger M., Bergamini A., Schmid B. & Joshi J. (2012): Profiteers of environmental change in the Swiss Alps: increase of thermophilous and generalist plants in wetland ecosystems within the last 10 years. – Alp. Bot. 122: 45–56.

Moravec J. & Rybníčková E. (1964): Die *Carex davalliana*-Bestände im Böhmerwaldvorgebirge, ihre Zusammensetzung, Ökologie und Historie. – Preslia 36: 376–391.

Navrátil J. & Navrátilová J. (2007): Wetlands succession in Ruda Nature Reserve, Czech Republic. – In: Okruszko S. T., Maltby E., Szatyłowicz J., Świątek D. & Kotowski W. (eds), Wetlands: monitoring, modelling, management, p. 27–36, Taylor & Francis Group, London.

Navrátilová J. & Navrátil J. (2005a): Stanovištní nároky ohrožených a vzácných rostlin rašelinišť Třeboňska [Environmental factors of some endangered and rare plants in Třeboňs mires]. – Zpr. Čes. Bot. Společ. 40: 279–299.

Navrátilová J. & Navrátil J. (2005b): Hlavní typy nelesní rašeliništní vegetace Třeboňské pánve [Main types of non-forest peat bog vegetation in the Třeboňská pánev basin]. – Sborn. Jihočes. Muz. České Budějovice, Přír. Vědy 45: 45–56.

Navrátilová J., Navrátil J. & Hájek M. (2006): Relationships between environmental factors and vegetation in nutrient-enriched fens at fishpond margins. – Folia Geobot. 41: 353–376.

Olde Venterink H., Wassen M. J., Verkroost A. W. M. & de Ruiter P. C. (2003): Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. – Ecology 84: 2191–2199.

Pasquet S., Pellerin S. & Poulin M. (2015): Three decades of vegetation changes in peatlands isolated in an agricultural landscape. – Appl. Veg. Sci. 18: 220–229.

Paulissen M. P. C. P., Besalú L. E., de Bruijn H., van der Ven P. J. & Bobbink R. (2005): Contrasting effects of ammonium enrichment on fen bryophytes. – J. Bryol. 27: 109–117.

Paulissen M. P. C. P., Schaminée J. H. J., During H. J., Wamelink G. W. W. & Verhoeven J. T. A. (2014): Expansion of acidophytic late-successional bryophytes in Dutch fens between 1940 and 2000. – J. Veg. Sci. 25: 525–533.

Pechar L., Přikryl I. & Faina R. (2002): Hydrobiological evaluation of Třeboň fishponds since the end of the nineteenth century. – In: Květ J., Jeník J. & Soukupová L. (eds), Freshwater wetlands and their sustainable future: a case study of the Třeboň Basin Biosphere Reserve, Czech Republic, p. 31–61, UNESCO and The Parthenon Publishing Group, Paris.

Peterka T., Plesková Z., Jiroušek M. & Hájek M. (2014): Testing floristic and environmental differentiation of rich fens on the Bohemian Massif. – Preslia 86: 337–366.

Rozbrojová Z. & Hájek M. (2010): Can tissue element concentration patterns at the individual species level indicate the factors underlying vegetation gradients in wetlands? – J. Veg. Sci. 21: 355–363.

Růžička I. (1989): Výsledky záchranného výzkumu ohrožené květeny mizejících rašelinišť a rašelinných luk na Jihlavsku [The results of rescue research of endangered flora of disappearing mires and mire meadows in the Jihlavsko region]. – Vlastiv. Sborn. Vysočiny, Odd. Věd Přír. 9: 135–176.

Rybníček K. (1970): *Rhynchospora alba* (L.) Vahl., its distribution, communities and habitat conditions in Czechoslovakia. – Folia Geobot. Phytotax. 5: 145–162 & 221–263.

Rybníček K. (1974): Die Vegetation der Moore im südlichen Teil der Böhmisch-Mährischen Höhe. – Vegetace ČSSR A6, Academia, Praha.

Schenková V., Čáp Hlaváč J. & Horsák M. (2013): Vrkoč rašelinný – další z glaciálních reliktů. Z červené knihy našich měkkýšů [*Vertigo lilljeborgi*: another glacial relict. From the Red book of our molluscs]. – Živa 61: 73–74.

Seer F. K. & Schrautzer J. (2014): Status, future prospects, and management recommendations for alkaline fens in an agricultural landscape: a comprehensive survey. – J. Nat. Cons. 22: 358–368.

Štechová T., Hájek M., Hájková P. & Navrátilová J. (2008): Comparison of habitat requirements of the mosses *Hamatocaulis vernicosus*, *Scorpidium cossonii* and *Warnstorfia exannulata* in different parts of temperate Europe. – Preslia 80: 399–410.

Štechová T., Holá E., Gutzerová N., Hradílek Z., Kubešová S., Lysák F., Novotný I. & Peterka T. (2010): Současný stav lokalit druhů *Meesia triquetra* a *Paludella squarrosa* (*Meesiaceae*) v České republice [Current state of localities of *Meesia triquetra* a *Paludella squarrosa* (*Meesiaceae*) in the Czech Republic]. – Bryonora 45: 1–11.

Štechová T. & Kučera J. (2007): The requirements of the rare moss, *Hamatocaulis vernicosus* (*Calliergonaceae, Musci)*, in the Czech Republic in relation to vegetation, water chemistry and management. – Biol. Cons. 135: 443–449.

Štechová T., Kučera J. & Šmilauer P. (2012): Factors affecting population size and vitality of *Hamatocaulis vernicosus* (Mitt.) Hedenäs (*Calliergonaceae*, *Musci*). – Wetlands Ecol. Manage. 20: 329–339.

Swinehart A. L. & Parker G. R. (2000): Palaeoecology and development of peatlands in Indiana. – Am. Midl. Nat. 143: 267–297.

Szurdoki E., Márton O. & Szövényi P. (2014): Genetic and morphological diversity of *Sphagnum angustifolium*, *S. flexuosum* and *S. fallax* in Europe. – Taxon 63: 237–248.

Tahvanainen T. (2004): The growth of *Scorpidium revolvens* in relation to calcium and magnesium. – Lindbergia 29: 123–128.

Vicherová E., Hájek M. & Hájek T. (2015): Calcium intolerance of fen mosses: physiological evidence, effects of nutrient availability and successional drivers. – Persp. Pl. Ecol. Evol. Syst. (in press, doi:10.1016/j.ppees.2015.06.005).

Wheeler B. D. & Proctor M. C. F. (2000): Ecological gradients, subdivisions and terminology of north-west European mires. – J. Ecol. 88: 187–203.

Zechmeister H., Tribsch A., Moser D. & Wrbka T. (2002): Distribution of endangered bryophytes in Austrian agricultural landscapes. – Biol. Cons. 103: 173–182.

Received 27 March 2015
Revision received 13 June 2015
Accepted 18 June 2015