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Changes in species richness and species composition of vascular plants and bryophytes along a moisture gradient

Změny druhové bohatosti a druhového složení cévnatých rostlin a mechorostů podél vlhkostního gradientu

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Dedicated to Kamil Rybníček and Eliška Rybníčková on the occasion of their 80th birthdays

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We focused on the gradient in moisture along transects of from 8 to 30 m in length from spring fen to semi-dry grassland vegetation. We selected an area in the calcium-rich part of the Western Carpathian flysch zone (Czech and Slovak Republics) where small spring-fed fens occur in close contact with semi-dry grasslands. Altogether 126 vegetation plots of 75 × 75 cm were sampled along 15 transects (one per locality) that each extended from the wettest part of a spring-fed fen into the surrounding semi-dry grassland. In addition, samples of standing plant biomass and soils were analysed for nutrients (N, P, K, C, Ca) and the upper-soil moisture measured. Using this study system and these sampling methods, we can test directly the effects of moisture and so avoid the confounding effects of different background environmental conditions that occur when data from many distinct sites is used. Data were processed using linear mixed-effect models and other statistical techniques. The trend in the number of species of vascular plants was unimodal with the optimum skewed towards lower moisture values. This response was not caused by an edge effect alone as replacing the moisture gradient with the positions of plots on transects resulted in a much weaker unimodal relationship and there was a group of species that occurred mainly in the species-richest moderately moist plots but did not occur in fens or the driest grasslands. The correlations between species richness and productivity (positive) and soil calcium (negative) differed from most of those reported in the literature, which suggests that the observed relationship between species richness and moisture was probably not greatly confounded by these factors. Species richness correlated negatively and the percentage of endangered species positively with the N:P biomass ratio, which is in accordance with other published results, but their correlations with moisture were stronger. For bryophytes, species richness linearly decreased towards the dry plots and did not correlate with any of the nutrients measured. Most of the species of vascular plants and bryophytes in the wettest patches were fen specialists, while more generalists made up the species richness in grasslands, including the species-richest patches. For bryophytes, the percentage of specialists was very high in fen plots. Although Mantel tests showed that bryophyte and vascular plant species turnovers were similar, we recorded substantial differences in their species richness patterns. Comparison with the results of a previous study on molluscs revealed a greater similarity between bryophytes and molluscs than between molluscs and vascular plants in terms of correlations between species richness and environmental variables. We argue that soil moisture should be taken into account when explaining current patterns in diversity in extremely rich temperate grasslands.

Keywords: *Caricion davallianae*, *Festuco-Brometea*, nutrients, productivity, semi-dry grassland, specialist, species density, spring fen, transect, White Carpathians

Introduction

Soil moisture is one of the most important environmental factors affecting plant species physiognomy and physiology and, as a consequence, species composition and diversity of plant communities. The variation in species richness along a moisture gradient is much less often recorded than the variation along gradients in terms of pH, productivity or availability of nutrients (for the most recent studies see, e.g. Cachovanová et al. 2012, Güssewell et al. 2012, Merunková & Chytrý 2012, Araya et al. 2013, Klaus et al. 2013, Kuiters 2013).

The variation in species richness along gradients of moisture are recorded predominantly for floodplain or riparian vegetation (e.g. Wassen et al. 2002, Dwire et al. 2004, Loheide & Gorelick 2007) and within mires (Navrátilová et al. 2006, Jabłońska et al. 2011). Studies along small-scale spatial gradients and on species-rich semi-terrestrial vegetation are rare (e.g. Flintrop 1994, Zelnik & Čarni 2008, Williams et al. 2011). We therefore selected a calcareous area in the Western-Carpathian flysch zone, where small fens occur in close proximity with moist, semi-dry and dry grasslands and therefore the effect of moisture can be studied along rather long gradients (Hettenbergerová & Hájek 2011, Schamp et al. 2011, Hettenbergerová et al. 2013). Spring-fed fens in that area belong to threatened central-European habitats because of their small area and specific environmental conditions. Despite their small area, they harbour a high number of endangered species for which their exact dependence on the level of moisture is unknown. Further, carrying out this research in this region has another advantage. White-Carpathian semi-dry grasslands are famous for their extremely species-rich grasslands (Klimeš et al. 2001, Wilson et al. 2012), which results from their history (Hájková et al. 2011) and a unique combination of abiotic factors and management (Merunková et al. 2012). While some authors (Klimeš 2008, Merunková et al. 2012) have speculated that the high species richness of some Carpathian grasslands is determined by intermediate moisture levels, no study has directly tested the species richness-moisture relationships along a long moisture gradient in this region.

Not only high levels of moisture, but also low availability of nutrients may explain the occurrence of rare species in calcareous fens (Wassen et al. 2005). In the White Carpathians there are high levels of calcium carbonate in tufa-forming spring-fed fens, which accounts for the low availability of phosphorus for vascular plants growing in these fens (Rozbrojová & Hájek 2008). There are species that can survive in these extreme ecological conditions for which each fen is an island refuge in an otherwise rather dry landscape (Horsák et al. 2012, Kapfer et al. 2012). Low availability of nutrients and permanent high ground-water level determine the high biomass of bryophytes growing in these fens (Hájková & Hájek 2003), whereas the semi-dry grasslands are dominated by vascular plants (Škodová et al. 2011). It is, therefore, possible to compare the moisture driven diversity patterns for two contrasting taxonomic groups. Only a few studies have directly compared the response of more groups of organisms, sampled in the same plots, to the moisture gradient. Such comparisons lead to more general conclusions about the relationships between soil moisture and biological diversity. In a previous study on the same system the moisture-driven diversity pattern of molluscs was studied (Dvořáková & Horsák 2012 within semi-dry grasslands; Hettenbergerová et al. 2013 along the fen-to-grassland gradient). Patterns in bryophyte, vascular plant and mollusc species composition and richness along a moisture gradient have not been previously directly compared. Generally speaking, bryophytes and vascular plants in fens are more often compared with respect to the pH/calcium gradient (Hájek et al. 2011, Sekulová et al. 2011, 2012) than the moisture gradient. The expectation is that their behaviour with respect to moisture will differ in terms of traits such as body size, type of reproduction, propagule dispersal, nutrient uptake and water use efficiency (Kapfer et al. 2012, Street et al. 2012).

The main questions addressed in this study were: (i) How does species richness and species composition of vascular plants and bryophytes change along a gradient of moisture from semi-dry grasslands to spring-fed fens? (ii) Which environmental factors are correlated with the fen-to-grassland gradient? (iii) Is there any difference between the species richness and species composition patterns of vascular plants, bryophytes and molluscs (identified in a previous study)? (iv) Is high species richness determined more by the numbers of specialists or generalists?

Study area

The study area is situated on the border between the Czech and Slovak Republics in the White Carpathians and Vsetínské vrchy Mts, which are a part of the Outer West Carpathians. The localities are at altitudes between 330 and 550 m a.s.l. Annual mean temperature in this area is about 7.5 °C and annual mean precipitation is approximately 700 mm. The bedrock in this area is formed by flysh, which is composed of alternating clay stones and sandstones, which means it is possible to have wetland and semi-dry grassland communities close to together. The localities were chosen in order to have as long as possible within-site gradient in moisture. At each locality there was a steep gradient in moisture from the fen to the semi-dry grassland. The vegetation in the fens belonged to the *Caricion davallianae* alliance and that in the surrounding semi-dry grasslands to the *Festuco-Brometea* class (alliance *Cirsio-Brachypodion pinnati* or *Bromion erecti*). Ecotonal communities classified within *Calthion* alliance occurred at some localities between fens and grasslands.

Nomenclature of the vegetation follows Chytrý (2007, 2011), that of vascular plants follows Danihelka et al. (2012) and of bryophytes Kučera et al. (2012).

Material and methods

Field sampling and environmental variables

Field data were collected in June and July during the years 2005–2008. At each of 15 localities one linear transect extended from the moistest part of the spring fen into the semi-dry grassland surrounding the fen with its central part in the transitional zone between fen and grassland. This zone in all cases was rather narrow and easily visible in the field as a structural ecotone, i.e. a steep transition between sedge-moss vegetation on wet soil to herbaceous plant-grass vegetation on dry soil. The number of plots sampled along each transect ranged from 5 to 16 and depended on the area of the fen. Altogether 126 plots were sampled. The size of plots was 75 × 75 cm and the distance between the centres of two neighbouring plots was two meters.

In each plot, species cover was estimated using a nine-grade scale (van der Maarel 1979). Both vascular plants and bryophytes were recorded. To obtain more information about nutrient limitations a sample of standing vascular plant biomass was taken from a 25 × 25 cm subplot in the centre of each plot. An upper soil sample was also taken. Moisture in the upper layer of the soil horizon (approximately 10 cm) was measured in each plot, always throughout the study area during a dry summer period (between July and September), using a moisture meter (ThetaProbe, soil moisture sensor ML2x). Concentrations of nitrogen, phosphorus, potassium and calcium in the dried and weighed vascular plant biomass were subsequently analysed; concentration of calcium and organic carbon were determined in soil samples. Before the chemical analyses, the samples of vascular plant biomass were air-dried at 70 °C. For the nitrogen determination, dry material was mineralized with sulphuric acid and hydrogen peroxide, and the nitrogen concentration determined by the distilling method using a Kjeltec apparatus. For determination of the other elements, material was mineralized in a sealed system, using microwave heating. Phosphorus concentration was determined spectrophotometrically, potassium concentration by atomic emission spectrophotometry and that of calcium by atomic absorption spectrophotometry (Zbíral 1994). Plant-available calcium in the soil was extracted using the Mehlich III (strong acid extraction with ion complex) method and determined using atomic absorption spectrophotometry. Organic carbon was determined by gravimetry (Zbíral 1995). Soil pH was not included in these analyses because the range of values was too narrow (pH_{H_2O} 6.0–8.0) as the soils in all the plots were base rich.

Data analysis

Relationships between species richness and the variables measured were statistically analysed using Spearman's rank correlation coefficient. A Bonferroni correction was used to correct for the problem associated with multiple testing. Relationships between particular environmental variables were evaluated using principal component analysis (PCA), applied to centered and standardized variables. Relationship between species richness (of vascular plants or bryophytes, respectively) and soil moisture measurements was evaluated using linear mixed-effect models, where soil moisture was included as quantitative fixed effect and locality (i.e. the transect) as a random effect. Both linear and polynomial types of relationship between species number and moisture were modelled and tested against each other to decide whether the shape of the relationship is linear or unimodal. To determine whether there is an edge effect on species richness, we analysed the relationship between number of species and standardized position of a plot along a transect. The plot positions along a transect were standardized to zero mean and unit variance in which the central plot, located on the fen-grassland transition, had a zero value, semi-dry grassland plots negative and fen plots positive values. The relationship was also analysed using linear mixed-effect models, in which the standardized position of a plot along a transect was included as a quantitative fixed effect and identity to locality (i.e. the transect) as a random effect. Both the linear and polynomial types of relationship were again tested against each other to determine the shape of the relationship.

Both the specialist vascular plants and bryophytes were selected using lists of diagnostic species for target classes, alliances and associations obtained from the analysis of a large vegetation-plot database for the Czech Republic in the Vegetation of the Czech Republic monograph (Chytrý et al. 2007, 2011). Thirty-eight species diagnostic for the *Scheuchzerio palustris-Caricetea nigrae* class, *Caricion davallianae* alliance and the

Valeriano dioicae-Caricetum davallianae and *Carici flavae-Cratoneuretum filicini* associations were considered to be fen specialists, whereas 60 species diagnostic of the *Festuco-Brometea* class, *Bromion erecti* and *Cirsio-Brachypodion pinnati* alliances and *Brachypodio pinnati-Molinietum arundinaceae* and *Scabioso ochroleucae-Brachypodietum pinnati* associations were considered to be semi-dry grassland specialists. One species, *Molinia arundinacea* s.s. (see Dančák et al. 2012 for taxonomic concept), was excluded from the semi-dry grasslands specialists because in the study area it occurs frequently also in fens. For the 181 remaining species was used the term "generalists". The relationship between percentage of specialists in the vegetation and moisture level was analysed using linear mixed-effect models (moisture a quantitative fixed effect and identity to locality a random effect). Only the linear regression model was tested, as testing polynomial model lacks theoretical justification. Relationships between number of specialist species and environmental variables were analysed using Spearman's rank correlation test with a Bonferroni correction. In the same way we analysed also the species richness and percentage of endangered species (categories C1–C4 in Grulich 2012).

Main ecological gradients were determined using detrended correspondence analysis (DCA) of square-root transformed data. Similarity between vascular plant and bryophyte matrices were compared using a Mantel test with square-root transformation based on Bray-Curtis distance and 999 permutations. Using data for the same 60 plots obtained in a previous malacological study (Hettenbergerová et al. 2013) we compared gradients of three different taxonomic groups: vascular plants, bryophytes and molluscs using a Mantel test based on the log-transformed data. All analyses were computed using the R program (version 2.15.2, R Core Team 2012).

Results

The soil moisture varied along the gradient studied (Electronic Appendix 1) from 18.8% in semi-dry grassland plots to 98.3% in fen plots. Vascular plant total species richness ranged from 8 to 53 species per plot, number of bryophyte species was between 0 and 13 per plot (Electronic Appendix 1). Regarding the relationship between number of vascular plant species and moisture, the polynomial model performed significantly better than the linear model ($P < 0.001$) and the polynomial model was significant ($P < 0.001$, Fig. 1) and had a unimodal shape with optimum shifted towards lower moisture values. The lowest species richness was recorded in the wettest plots, while the highest numbers of species were recorded in plots with intermediate-low moisture levels (37–60%). There were four maximum values for total number of bryophyte species over the same moisture range, but the general species richness-moisture relationship modelled using mixed-effect models was linear with a decrease towards dry plots ($P < 0.01$; Fig. 1). The polynomial model in this case was not significantly better than the linear one ($P = 0.078$). When the relationship between number of species and standardized plot position (i.e. the effect of the structural ecotone visible in the field) was tested, the relationship for vascular plants was unimodal (Fig. 2), although less clear than that of species richness along the moisture gradient, with the polynomial model significantly better than the linear ($P < 0.05$) and overall significant ($P < 0.001$). In the case of bryophytes the relationship was linear (overall significance of linear model $P < 0.05$, with polynomial model not significantly better with a value of $P = 0.148$).

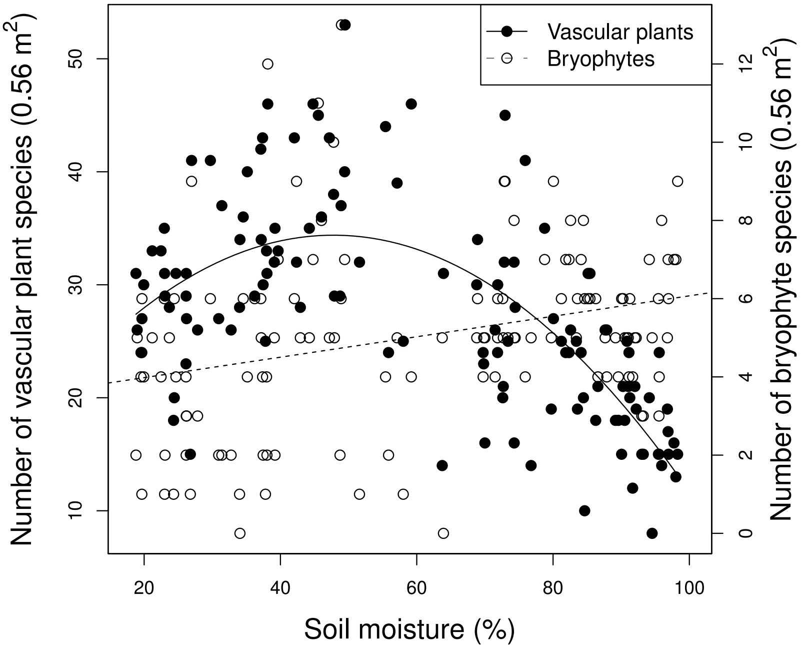


Fig. 1. – Relationships between species richness of vascular plants and bryophytes and soil moisture. The regression for vascular plants was fitted using polynomial and for bryophytes linear regression.

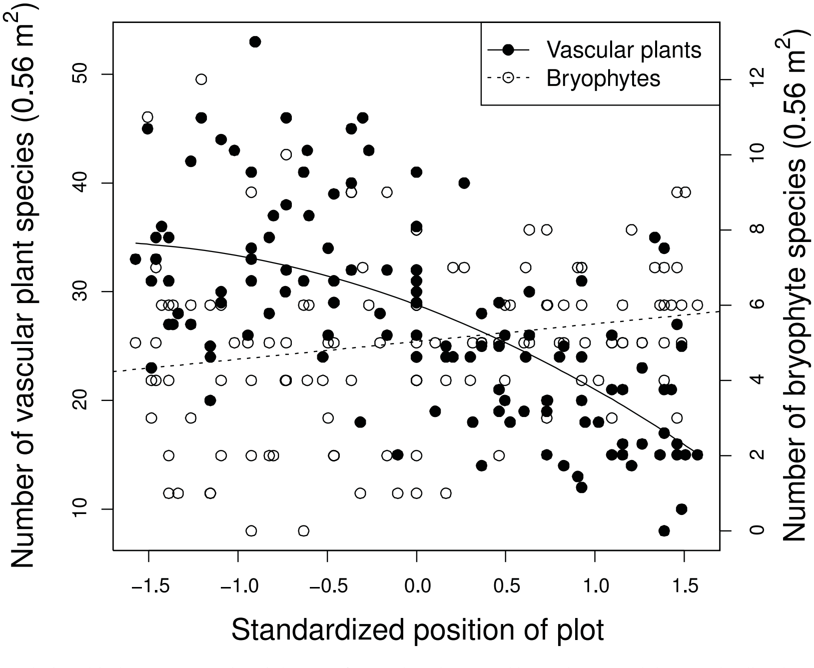


Fig. 2. – Relationship between species richness of vascular plants and bryophytes and the standardized position of the plots along the transects. Negative values refer to semi-dry grasslands and positive values to spring fens. The regression for vascular plants was fitted using polynomial and for bryophytes linear regression.

Table 1. – Values of Spearman rank correlations between species richness and the variables measured and their statistical significance. Significant correlations after Bonferroni correction are in bold ($P < 0.0071$).

	Number of vascular plant species						Number of bryophyte species					
	All species		Semi-dry grassland specialists		Spring fen specialists		All species		Semi-dry grassland specialists		Spring fen specialists	
	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
Soil												
Moisture	**– 0.57**	**<0.001**	**– 0.78**	**<0.001**	**0.76**	**<0.001**	**0.34**	**<0.001**	**– 0.45**	**<0.001**	**0.79**	**<0.001**
C	0.09	0.294	– 0.11	0.241	0.09	0.335	0.10	0.251	– 0.12	0.172	0.12	0.17
Ca	**– 0.66**	**<0.001**	**– 0.70**	**<0.001**	**0.62**	**<0.001**	0.02	0.805	**– 0.50**	**<0.001**	**0.60**	**<0.001**
Biomass												
Weight	**0.39**	**<0.001**	**0.34**	**<0.001**	– 0.21	0.02	– 0.18	0.05	0.10	0.273	**– 0.34**	**<0.001**
Ca	0.14	0.128	0.19	0.034	– 0.09	0.297	0.13	0.153	0.23	0.009	0.04	0.697
N:P	**– 0.50**	**<0.001**	**– 0.27**	**0.002**	**0.32**	**<0.001**	– 0.08	0.4	**– 0.26**	**0.003**	0.24	0.007
N:K	**– 0.49**	**<0.001**	**– 0.41**	**<0.001**	**0.29**	**<0.001**	0.02	0.863	**– 0.26**	**0.003**	**0.25**	**0.004**

Total species richness of vascular plants correlated also with the amount of calcium in the soil, weight of biomass (i.e. productivity) and biomass N:P and N:K ratios (Table 1). Nevertheless, all these variables correlated also with soil moisture (see Electronic Appendix 2, 3). Number of semi-dry grassland specialist species correlated with the same environmental variables as total species richness. Fen specialist species richness showed opposite correlations compared to total species richness. Number of bryophyte species was positively significantly associated only with soil moisture, but number of fen bryophyte specialists was positively also associated with soil calcium and N:K ratio and negatively with weight of vascular plant biomass. Semi-dry grassland bryophyte specialist species richness was negatively associated with soil moisture, soil calcium and biomass N:P and N:K ratios (Table 1).

Most of the vascular plant species recorded in the wettest patches were fen specialists (Fig. 3A) and the number significantly linearly decreased towards the dry patches ($P < 0.001$, Fig. 4). Only a few generalist or semi-dry grassland specialists occurred in fens. On the other hand, the high species richness in intermediate and dry plots is made up of not only semi-dry grassland specialists but also generalists. Bryophytes showed a similar and even more clear pattern ($P < 0.001$, Fig. 3B and 4), but there was only a small number of semi-dry grassland specialists. The species richness of endangered species of vascular plants correlated (Spearman rank correlation; $P < 0.00714$ after Bonferroni correction) only with soil moisture ($r_S = 0.403$), while percentage of endangered species correlated with soil moisture ($r_S = 0.648$), soil calcium ($r_S = 0.431$), N:P biomass ratio ($r_S = 0.346$), N:K biomass ratio ($r_S = 0.302$) and also with vascular plant species richness ($r_S = – 0.402$).

For each species we described its distribution pattern along the moisture gradient (Fig. 5). The most common species occurring along the whole moisture gradient were *Carex flacca* (recorded in 95 of the 126 plots), *Calliergonella cuspidata* (89) and *Festuca rubra* (84); other common species were *Equisetum arvense* (73), *Briza media* (69), *Plagiomnium affine* agg. (63) and *Tussilago farfara* (51). Species that occurred mainly in wet fen plots were fen specialists (e.g. *Triglochin palustre*, *Dactylorhiza majalis*, *Eriophorum*

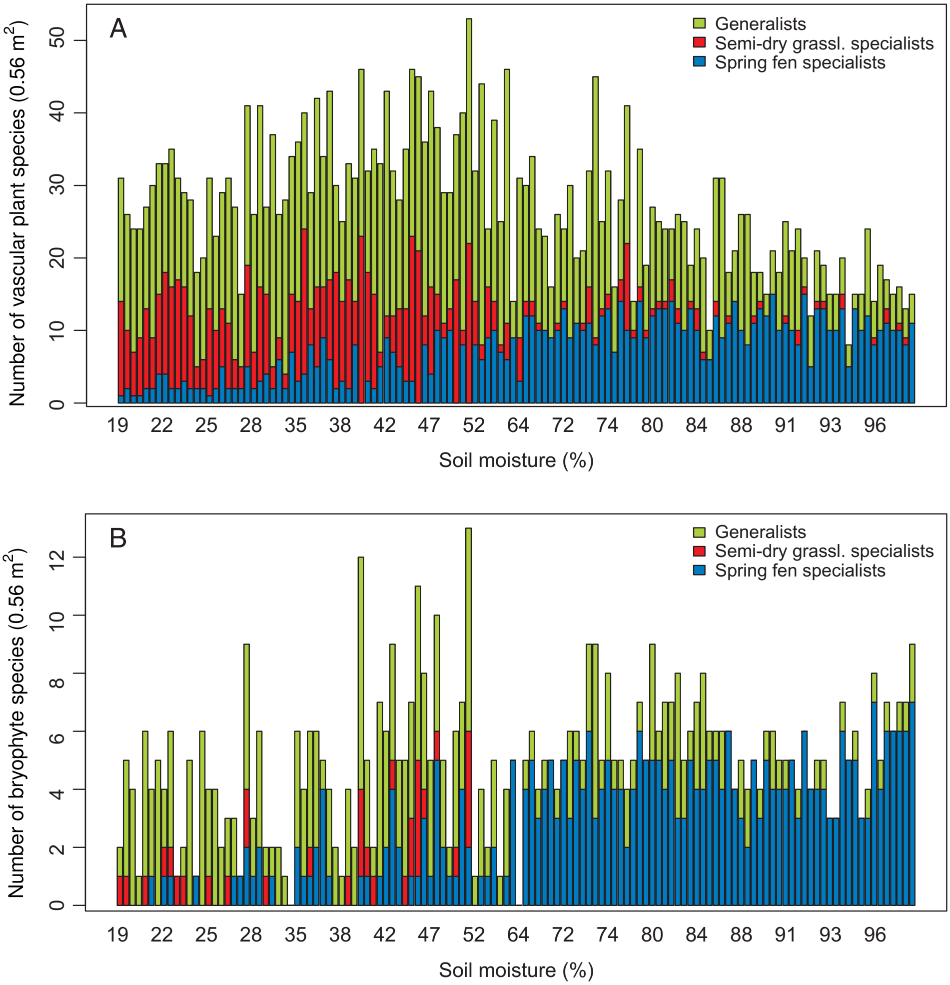


Fig. 3. – Numbers of species of (A) vascular plants, and (B) bryophytes. Each column represents one plot on the soil moisture gradient.

angustifolium, *E. latifolium*; *Philonotis calcarea*, *Palustriella commutata, Aneura pinguis*) and species that are not considered to be strict fen specialists and occur in many wetland habitats (*Crepis paludosa*, *Equisetum fluviatile*, *Mentha arvensis*). On the other hand, species that occurred mainly in the driest patches belong mostly to semi-dry grassland specialists (*Euphorbia cyparissias*, *Pimpinella saxifraga*, *Thymus pulegioides*, *Sanguisorba minor*; *Homalothecium lutescens, Fissidens dubius*). Some fen specialists, i.e. the species used as diagnostic of calcareous fen vegetation in Chytrý (2011), occurred along the entire moisture gradient (e.g. *Potentilla erecta*, *Carex flacca*, *Tussilago farfara*, *Briza media*; *Calliergonella cuspidata*).

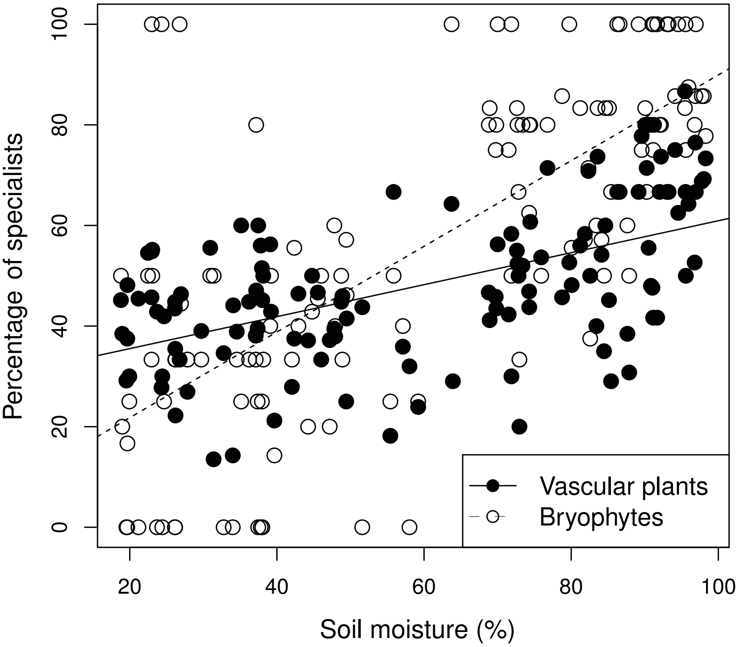


Fig. 4. – Relationship between percentage of the species that are specialists and soil moisture.

Only a few species had median values for moisture (calculated from the moisture measured at sites of their occurrence) between 50–70%, and all of them showed wide distribution along the moisture gradient (Fig. 6). There was a single species (*Carex lepidocarpa*) with median moisture between 50–80% and, simultaneously, with interquartile range lower than 20%. On the other hand very few species had middle median value and low interquartile range (Fig. 6). A group of species that inhabited grasslands and not fens occurred mainly in species-richest plots of rather intermediate moisture of between 37–60% (*Aquilegia vulgaris*, *Allium scorodoprasum*, *Anthoxanthum odoratum*, *Carex pallescens*, *Colchicum autumnale*, *Inula salicina*, *Rumex acetosa*, *Vicia tenuifolia*; *Ctenidium molluscum, Fissidens taxifolius, Rhytidiadelphus triquetrus*).

Remarkable changes in species composition of vascular plants and bryophytes were recorded along the moisture gradient. The species turnover from drier to wetter plots was high (the length of first DCA axis for vascular plants = 4.090 SD, for bryophytes = 2.776 SD). Mantel test revealed a highly significant correlation ($r = 0.561$, $P < 0.001$) between both vascular plant and bryophyte abundance matrices. Mantel test based only on 60 malacological plots showed in all three combinations of taxonomic groups highly significant relationships (vascular plants versus bryophytes: $r = 0.600$, $P < 0.001$, vascular plants versus molluscs: $r = 0.542$, $P < 0.001$, bryophytes versus molluscs: $r = 0.370$, $P < 0.001$).

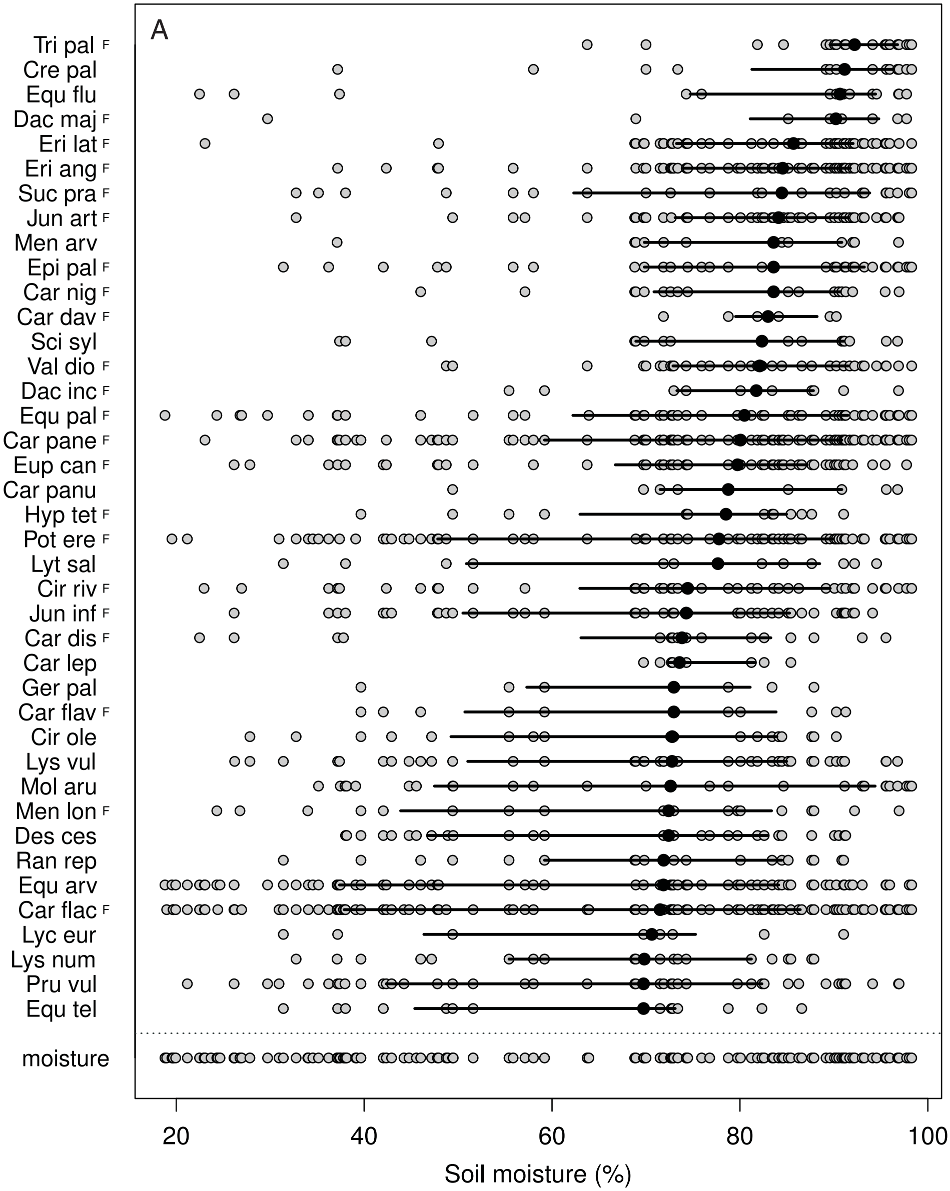
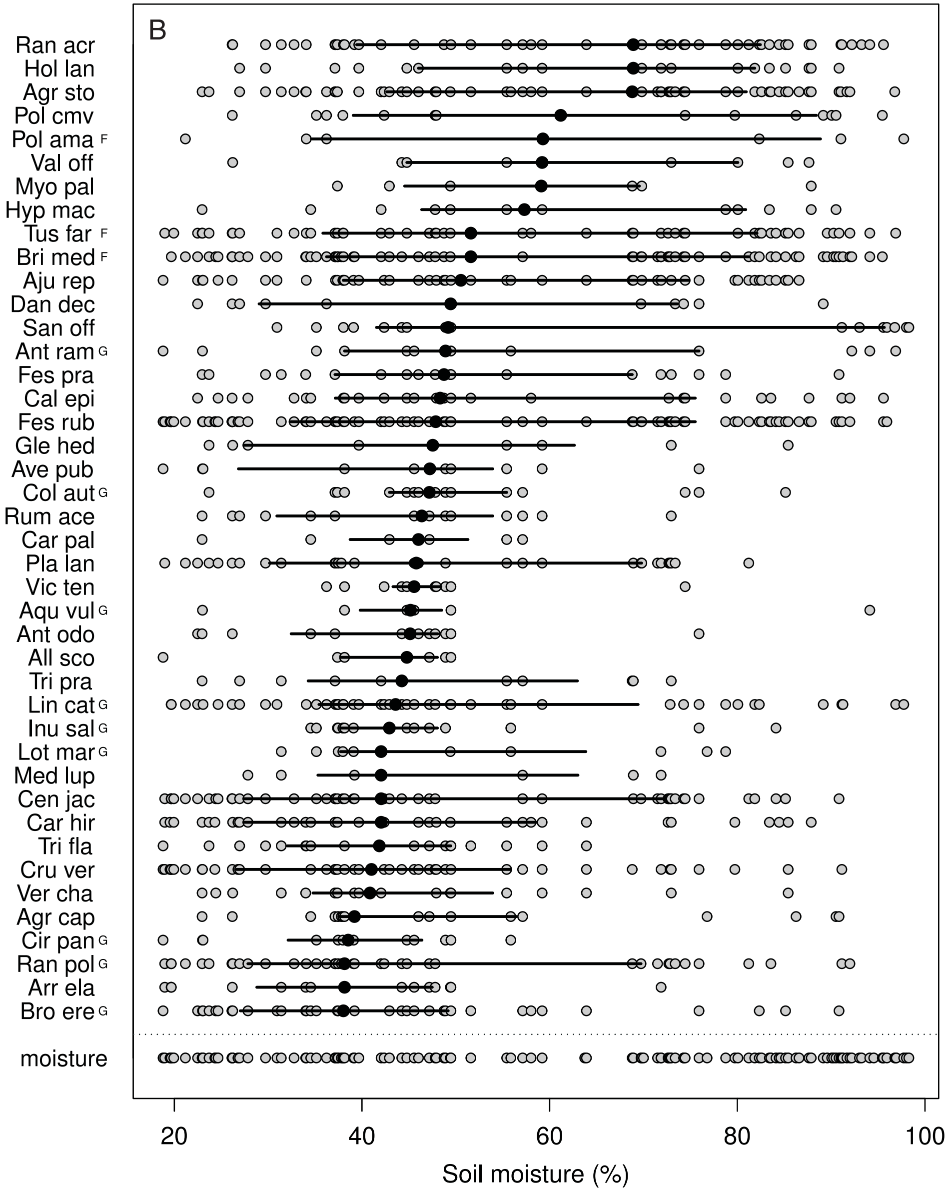


Fig. 5. – Occurrence of species of (A–C) vascular plants and (D) bryophytes along the soil moisture gradient. Median (black point), 25–75% quantile (interquartile, black line) and soil moisture measured where the species occurred (grey point) are displayed. Species are ordered by median values; for full species names see Electronic Appendix 4. Letter at the end of the abbreviation refers to either (F) spring fen or (G) semi-dry grassland specialists. Only species with a frequency > 6 and presence on two or more transects are displayed. Distribution of moisture values are shown at the bottom of the figure.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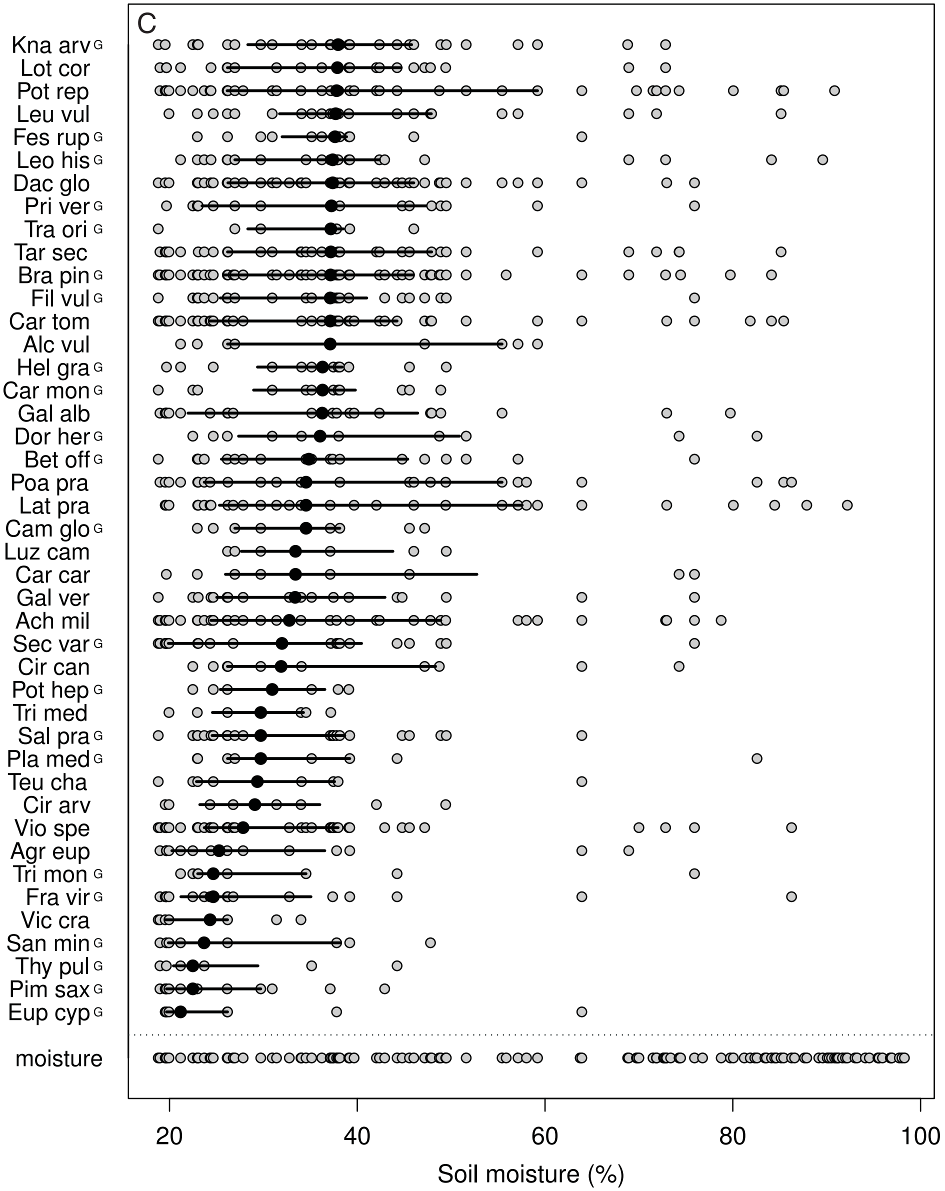
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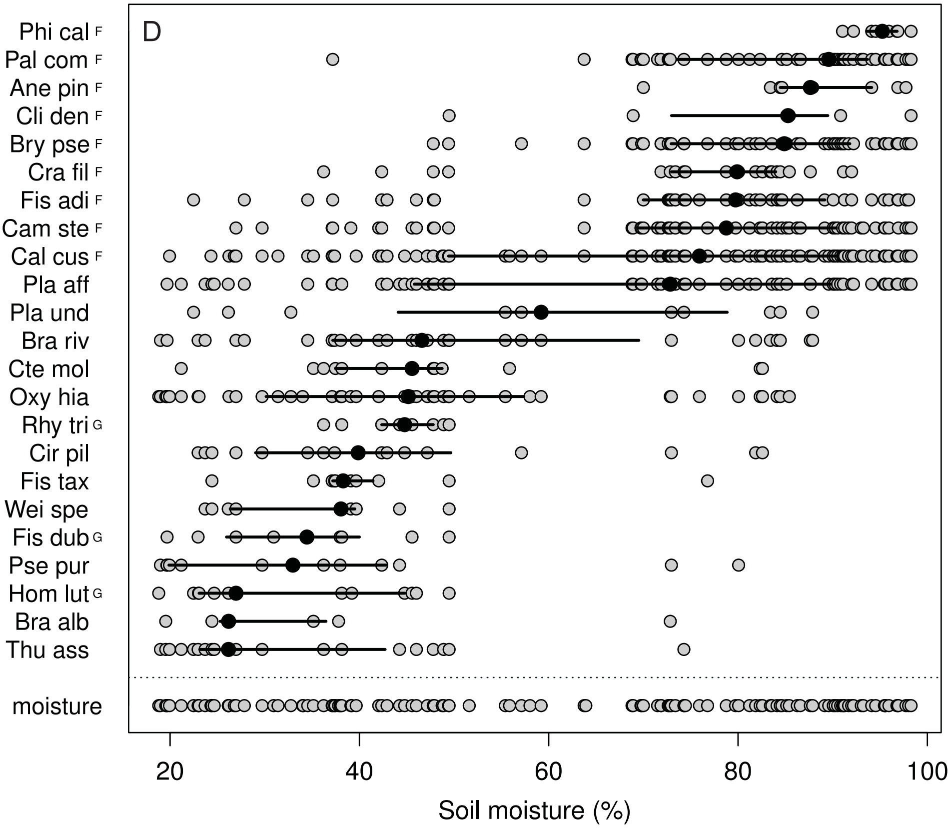

Discussion

The effect of moisture and possible confounding factors

The results confirmed our preliminary hypothesis that there would be more species of vascular plants and fewer species of bryophytes in semi-dry grasslands than fens (see also Hájková & Hájek 2003). However, the trend in the number of species of vascular plants did not peak in the driest parts of the grasslands, but was unimodal. This unimodal trend seems to be largely due to the effect of moisture per se and not an edge effect, which is frequently reported in the interface between forests and grasslands (Łuczaj & Sadowska 1997, Orczewska & Glista 2005) or between wetland and arid habitats (Hou et al. 2008). This presumption is supported by two pieces of evidence. First, there was only a weak and marginally significant unimodal relationship when a standardized plot position was used as an independent variable. Second, the occurrence of the group of species that characterize the richest plots was confined to particular moisture levels. The lack of an edge effect in the system studied (see also Hettenbergerová & Hájek 2011 for further evidence) refutes the hypothesis of Merunková et al. (2012) that source-sink dynamics in fen-grassland mosaics have a role in determining the high species richness of grasslands in the White Carpathians. Our results rather support the hypothesis that intermediate or fluctuating

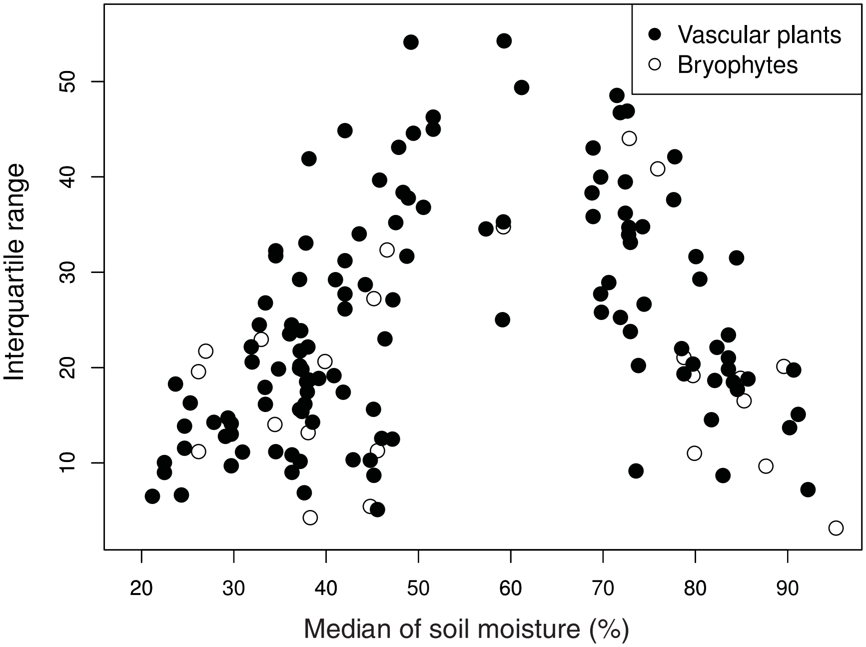

Fig. 6. – Relationship between median and interquartile range (for values see Fig. 5) for particular species of vascular plants and bryophytes.

moisture levels have a role in determining high local species richness in these grasslands, where mesophilous and moisture-demanding species coexist with xerophilous species (Klimeš 2008, Škodová et al. 2011, Merunková et al. 2012). At the extreme ends of the moisture gradient, species richness is restricted either by anoxia (fens) or seasonal drought (the driest grasslands).

The observed trend of species richness along the gradient of moisture does not appear to be affected by the confounding effects of different background environmental conditions when data for many distinct sites are used, which conforms to the results of a previous study on molluscs (Hettenbergerová et al. 2013). Although moisture and some of the other factors are inter-correlated, the correlations with moisture best explain the observed pattern in species distribution. Soil pH, the principal determining factor in many large-scale studies (Pärtel 2002), was similar in all the plots. Soil calcium correlated negatively with species richness in some cases, while in general the correlations between calcium and species richness are positive (Pärtel 2002, Cachovanová et al. 2012, Merunková & Chytrý 2012, Sekulová et al. 2012). Taking into consideration that the concentration of calcium along the entire moisture gradient was rather high (see also Hettenbergerová et al. 2013) we conclude that the result for calcium is because the values for calcium and moisture covary. In species-poor fens calcium is continuously supplied by spring water, while in surrounding grasslands calcium is slightly leached from the topsoil.

Also the correlation with productivity (biomass weight) is because it and moisture covary. We found a positive correlation between species richness and productivity, whereas most studies from analogous productivity levels record either no or a negative correlation (Vermeer & Berendse 1983, Wheeler & Shaw 1991, Bergamini et al. 2001, Hájková & Hájek 2003; but see Olde Venterink et al. 2001). The relationship between species richness and moisture recorded in our study conforms with the results of Dwire et al. (2004), who report a high species richness in dry grasslands and low species richness in wet grasslands, but the aboveground plant biomass correlated positively with moisture in Dwire's study and negatively in our study.

On the other hand, we cannot distinguish between the causal effects of moisture and phosphorus limitation on the species richness pattern. High N:P ratios, which we recorded mainly in fen grasslands, generally is inconsistently correlated with species richness (Güsewell 2004). Güsewell et al. (2005) recorded low species richness at sites with a high N:P ratio, as occurred in our study. That a high percentage of the species at sites with a high N:P are endangered corresponds with the results of studies by Wassen et al. (2005) and Pawlikowski et al. (2013), but the much stronger correlation with moisture recorded in our study suggests that the effect of moisture is more important. The complexity of the relationship between moisture, phosphorus limitation and species richness is highlighted by the causal relationship between moisture and phosphorus availability. The high amount of calcium carbonate in our fen grasslands makes phosphorus unavailable (Boyer & Wheeler 1989, Rozbrojová & Hájek 2008).

Distribution of specialists

The stress caused by both phosphorus limitation and anoxia due to high water levels in general favour specialists in fens while in drier grasslands competition favours generalists. Analogous results are reported by Zelnik & Čarni (2008) who record the same pattern for S-strategy and C-strategy species. The former correspond largely to specialists and the latter to generalists.

Based on an analysis of a large database, Fajmonová et al. (2013) report that there is a statistically significant overrepresentation of plant specialists in spring-fed fens and semi-dry grasslands in the Outer Carpathians, both of which were included in our study. The percentage of specialists in semi-dry grasslands was roughly equal to that in spring-fed fens. This discrepancy with our results is attributed to the different methods used to identify the specialist and different scales used in these two studies. The use of small plots in our study probably resulted in an overestimate of local environmental filtering over species pool effects, which were more important in the study of Fajmonová et al. (2013). Further, our result that the species richness of semi-dry grasslands was largely governed by generalists also differs from that generally reported in the literature (Öster et al. 2007, Cachovanová et al. 2012). Again, different methods of identifying specialists may be the reason, as we considered only the specialists that occur in *Bromion erecti* and *Cirsio-Brachypodion pinnati* grasslands.

Cross-taxon comparison

The contrasting patterns recorded for vascular plant and bryophyte species richness along the moisture gradient could be explained in terms of competition between these two groups. As bryophytes can absorb nutrients directly from water through their whole surface, they can survive in nutrient-poor, but waterlogged fen habitats. Because vascular plants produce less biomass here, bryophytes can cover up to 100% of the ground in these habitats. This is in accordance with the results recorded for Estonian species-rich dry calcareous grasslands, where bryophyte productivity was negatively associated with vascular plant productivity (Niinemets & Kull 2005). In addition, in our study there was a strong overrepresentation of specialist bryophytes in fens, suggesting more intense environmental filtering in fens. This difference between vascular plants and bryophytes confirms the result of the large-scale study of Hájek et al. (2011). Although the pattern of species richness recorded along the moisture gradient differed for the taxonomic groups studied, Mantel tests revealed a highly significant correlations between all three abundance matrices (vascular plants, bryophytes and molluscs), which indicates similar rates of species turnover along the gradient studied.

In a previous study, species richness of molluscs was not correlated with the moisture gradient or any other environmental variable except for biomass weight (Hettenbergerová et al. 2013). This result corresponds more to that recorded for bryophytes than for vascular plants as overall bryophyte species richness was correlated only with moisture (but linearly so, in contrast to vascular plants). The reasons why the densities of bryophytes and molluscs species vary differently may include smaller body size associated with a dependence on small-scale structural properties such as microclimate or the shaded conditions that prevail under a vascular-plant canopy, lack of large underground organs, shorter life span and greater mobility (Horsák et al. 2012). We found remarkable changes in species composition along the gradient for vascular plants, bryophytes and molluscs. First DCA axes of vascular plant, bryophyte (this study) and molluscan (Hettenbergerová et al. 2013) species data were long, which indicates the data is heterogeneous and there was a high species turnover along the moisture gradient.

Individual species performance along the moisture gradient

The most frequent species, i.e. the species with highest tolerance of the variability in moisture (Fig. 5), was *Carex flacca*. This species is often recorded not only in rich-fen grasslands (Hájková et al. 2004, Hájek et al. 2013) but also in various types of semi-dry grasslands (e.g. Chytrý et al. 2007, Dúbravková et al. 2010, Škodová et al. 2011). Another common species with a wide moisture tolerance, *Calliergonella cuspidata* and *Briza media*, are usually classified as either wetland or dry-grassland species, respectively (Chytrý 2011). Their wide tolerance of moisture recorded in this study is similar to that recorded by other studies carried out in the same region (Rozbrojová & Hájek 2008, Hájek et al. 2013). The importance placed on the diagnostic value of these species in the vegetation survey of the Czech Republic (Chytrý 2011) is therefore not valid at the scale of the calcareous areas in the Western-Carpathian flysch zone.

The individual species' performances along the moisture gradient result in a unimodal species richness pattern for vascular plants, the organisms whose richness in the study area is exceptional globally (Wilson et al. 2012). Directly measured moisture levels were not included in the studies that attempted to account for the extremely high species richness of temperate grasslands. Our results suggest that further research on this topic should include detailed measurements of moisture.

See www.preslia.cz for Electronix Appendices 1–4

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Souhrn

V této práci jsme se zaměřili na vlhkostní gradient vedoucí z prameništní vegetace do travinné. Pro studium jsme si vybrali vápnitou oblast Bílých Karpat a Vsetínské hornatiny na území České a Slovenské Republiky, kde se v komplexech širolistých suchých trávníků vyskytují malá pěnovcová prameniště. Na 15 lokalitách (transektech) jsme zapsali celkem 126 malých vegetačních snímků o velikosti 75 × 75 cm. Transekt vedl vždy z nejvlhčího místa prameniště přes jeho okraj do suchého trávníku. Pro stanovení množství živin (N, P, K, C, Ca) jsme odebírali vzorky půdy a biomasy a také jsme měřili vlhkost horní vrstvy půdy. Data byla vyhodnocena různými statistickými metodami včetně lineárních modelů se smíšenými efekty. Tento metodický postup nám umožnil přímo testovat čistý vliv vlhkosti na druhovou bohatost, bez výrazného ovlivnění rozdíly mezi lokalitami a jinými faktory prostředí. Počet druhů cévnatých rostlin vykazoval unimodální odpověď s optimem posunutým do nižších hodnot vlhkosti. Tento výsledek však nebyl zapříčiněn jen vlivem okrajového efektu, neboť po nahrazení půdní vlhkosti standardizovanou pozicí plochy na transektu byla odpověď unimodální jen slabě. Dalším argumentem proti vysvětlení tohoto výsledku vlivem okrajového efektu je existence druhů, které upřednostňovaly spíše středně suchá a druhově bohatá místa, a zároveň se nevyskytovaly ani v prameništích ani v sušších loukách. Korelace mezi počtem druhů a produktivitou (pozitivní) a vápníkem v půdě (negativní) se lišily od většiny výsledků uváděných v literatuře, což ukazuje, že vztah mezi vlhkostí a druhovou bohatostí pravděpodobně nebyl v našem datovém souboru těmito faktory ovlivněn. V případě korelací s poměrem N:P v biomase, který indikuje úroveň limitace produktivity přístupností fosforu, jsme v souladu s jinými studiemi zjistili negativní vztah k celkovému počtu druhů a pozitivní vztah k zastoupení ohrožených druhů; vlhkost půdy však s těmito proměnnými korelovala silněji. Druhová bohatost mechorostů lineárně klesala směrem k suchým loukám a nekorelovala s žádnými měřenými prvky. Na prameništích tvořili druhovou bohatost cévnatých rostlin i mechorostů specialisté, zatímco velký počet druhů v sušších trávnících, včetně druhově nejbohatších ploch, byl tvořen spíše generalisty. V případě mechorostů stoupal podíl specialistů směrem do vlhka prudčeji než tomu bylo u cévnatých rostlin. Ačkoli změny druhového složení mechorostů a cévnatých rostlin podél vlhkostního gradientu spolu korelovaly (Mantelův test vyšel silně signifikantně), prokázali jsme značný rozdíl ve změnách druhové bohatosti. Domníváme se, že půdní vlhkost by měla být častěji brána do úvahy při vysvětlování diverzity temperátní travinobylinné vegetace.

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