Comparison of habitat requirements of the mosses *Hamatocaulis vernicosus*, *Scorpidium cossonii* and *Warnstorfia exannulata* in different parts of temperate Europe

Porovnání stanovištních nároků mechů *Hamatocaulis vernicosus*, *Scorpidium cossonii* a *Warnstorfia exannulata* v různých částech temperátní Evropy

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Habitat affinities of the red-listed and EU Habitat Directive moss species *Hamatocaulis vernicosus* and the more widely distributed allied species *Scorpidium cossonii* and *Warnstorfia exannulata* were analysed. Ecological preferences of these fen mosses, with respect to water pH, water conductivity, Ellenberg's moisture and nutrient indicator values, were compared in three different European locations (Bohemian Massif, the West Carpathians and Bulgaria) using logistic regressions fitted by means of Huisman-Olff-Fresco models. Inter-specific co-occurrences of the species were also investigated. *Warnstorfia exannulata* preferred slightly acid conditions, about pH 5.6 at all the locations studied. Ecological behaviour of *S. cossonii* was very similar at all the locations, where it occupied base-rich habitats (pH > 7). The pH optimum of *H. vernicosus*, occupying habitats in the middle part of the base richness gradient, varied between locations from 6.0 in Bulgaria to 6.7–7.0 in the West Carpathians and Bohemian Massif. Niche diversification followed the gradient in Ellenberg nutrient indicator values and was similar at all the locations. In the Bohemian Massif and Bulgaria, the occurrence of *W. exannulata* was further associated with a relatively high moisture indicated by the Ellenberg indicator value. The results obtained from the Huisman-Olff-Fresco models accord with the results of inter-specific co-occurrences. Moreover, the latter method revealed a link between *H. vernicosus* and the occurrence of disjunctly occurring boreal sedges, suggesting the relic nature of *H. vernicosus* habitats at these locations.

Keywords: brown mosses, bryophyte, *Drepanocladus*, fen, HOF modelling, mineral richness, mire, niche diversification, water pH

Introduction

Hamatocaulis vernicosus is a red-listed moss species throughout most of Europe and particularly in the Central European region, attaining even the official listing of the Bern Convention (Council Directive 92/43/EEC 1992). An increasing focus on *Hamatocaulis vernicosus* because of its protected status by EU Habitat Directive in network Natura 2000 led to a more detailed exploration of its habitat requirements in Europe. The species occurs in fens, where it can dominate together with the closely related species *Scorpidium cossonii* and *Warnstorfia exannulata*, and other brown mosses (Bergamini et al 2001, Hájek et al. 2006). All three species are similar with respect to growth type but their niche diversification is less known than that of other important mire genera such as *Sphagnum* (e.g., Daniels & Eddy 1990, Bragazza 1997, Hájková & Hájek 2004, 2007) or *Philonotis* (Hájková et al. 2007). Even though a clear ecological separation of these species along a pH gradient is reported for the boreal zone (Janssens 1983, Hedenäs & Kooijman 1996), they often grow together in Central Europe (Štechová & Kučera 2007). In other parts of Europe, little is known about the habitat affinities of these three important fen species.

Previous studies on the habitat preferences of the three species studied (Janssens 1983, Hedenäs & Kooijman 1996, Hedenäs 2003) have mostly been done in the boreal and boreoatlantic zone, where their habitat preferences were compared by means of ranges and medians of environmental factors measured in tufts of these mosses. The objective of our study is to model the realized niches of the species in terms of complete environmental gradients. We use field data from SE Europe (Bulgarian mountains), where these species have not been previously investigated and data from two contrasting Central-European locations (the Bohemian Massif and the West Carpathians), for which only incomplete information is available (Hájková 2005, Štechová & Kučera 2007). In the West Carpathians, calcareous fens are the most frequent mire habitat (Hájek et al. 2007). Acidic fens are more common at the two other locations, especially in the cold mountains in Bulgaria (Hájková & Hájek 2007).

In this paper, we address the question how the realized niches of these species differ in areas where both the commonness of particular habitats and the relative frequency of the species differ. According to the evolutionary species pool hypothesis (e.g., Pither & Aarssen 2005, Hájek et al. 2007), ecological optima and amplitudes of species differ due to differences in the incidences of acidic and base-rich habitats, and according to the theory of competitive release (e.g., Coudun & Gégout 2005), species should occupy a different or have a wide realized niche, when there are fewer competitors. Finally, the results of species response curve modelling is compared with inter-specific co-occurrences of these species.

Materials and Methods

Study area

These species were studied in the Bohemian Massif in the Czech Republic (BM), the West Carpathians in Slovakia, Czech Republic and Poland (WC) and the Bulgarian mountain ranges (BG). In BM, the localities are predominantly in the Třeboňská pánev basin and Českomoravská vrchovina highland (cf. Štechová et al. 2007), where there is an abundance of natural mires and springs. A few of the localities are scattered over the entire BM, which includes a major part of the Czech Republic, except for the easternmost part. The geological bedrock of BM is formed predominantly of metamorphosed schists (phyllite, mica schist, gneiss, amphibolite) permeated by granites. In WC (Slovakia, Poland, Czech Republic), most of the samples originate from the flysch bedrock, where geological strata (bed) of sandstone and claystone alternate and differ both in chemistry and proportion of sandstone and claystone. However, data for other bedrocks such as limestone or granite are also included in the study. In BG, mires were investigated in mountains where mires naturally occur (e.g., Rhodopes, Rila, Pirin, Stara Planina, Vitosha, Osogovska Mt, Sredna

Gora Mts). Granite, gneiss, granodiorite, sandstone, claystone, siltstone, metamorphosed shale, marble and limestone form the bedrock at particular study regions. All the study sites are located within the temperate climate zone. BM has a more oceanic climate compared to the other two locations, with mean annual temperatures mostly between 4 and 8 °C, and precipitation sum mostly between 600 and 900 mm per year (Tolasz 2007). In WC, mean annual temperatures at the study sites were between 3 and 7.5 °C in most cases (mean for all sites 5.2 °C) and precipitation sums mostly between 750 and 1100 mm (mean for all sites 940 mm). The climate in BG is continental, only locally influenced by the Mediterranean. Climatic data are not available for the majority of the study sites. The rate of evaporation at high temperatures at altitudes up to ca 1000 m a.s.l. (mean annual temperature 10 °C or more, precipitation sum about 600–700 mm) is not suitable for the development of *Sphagnum* mires (Hájková & Hájek 2007). The altitudinal belt of ca 1300–1800 m a.s.l. corresponds to the Central-European beech and spruce vegetation belts and contains most types of mire, except for subalpine and alpine mires. The climate of the subalpine and alpine zones in the Bulgarian high-mountains (mostly above 1800 m a.s.l.) is cold and humid. The mean annual precipitation on the highest peaks varies around 1000 mm and the mean annual temperature around –2 °C (Lieth et al. 1999). Of the species studied, only *W. exannulata* was found in the (sub)alpine wetlands.

Field data sampling

Samples of vegetation were collected from springs and mires in BM, WC and BG in growing periods in 2001–2005. At lower altitudes, most samples were collected between the end of May and beginning of July, but in the high mountains between the end of June and September. For the numbers of the samples collected in each area see Table 1. All vegetation-plot and environmental data from mires were included in the analysis, regardless of whether they contained the target species (see Vetaas 2000, Hájková et al. 2007 for the advantages of this method). An area of 16 m^2 was sampled in most cases; plots that were obviously heterogeneous in terms of superficial structure, vegetation type or physical-chemical properties of the water were avoided. Cover of all species was estimated using the nine-grade Braun-Blanquet scale (van der Maarel 1979).

Water conductivity and pH, both standardized at 20°C, were measured in situ using portable instruments. Water conductivity (ln-transformed) accurately reflects the mineral richness (Ca+Mg) of the groundwater, especially in spring-fed mires (Sjörs & Gunnarson 2002; Hájek & Hekera 2004). Conductivity due to H^+ ions was subtracted for acidic waters with a pH < 5.5 (Sjörs 1952). Both these physical-chemical factors (pH, conductivity) are relatively stable over time compared to other factors such as iron or phosphorus concentrations, and separate major fen types throughout the season (Vitt et al. 1995, Tahvanainen et al. 2003, Hájek & Hekera 2004, Hájek et al. 2005). In spring fens, the measurements were of the water surrounding the mosses. When the water level was several centimetres below the surface, a small shallow pit was dug and water allowed to clarify before measurement. On the basis of the composition in the vegetation samples, the Ellenberg indicator values for moisture and nutrients were calculated as unweighted means of all vascular plant species present in vegetation plots.

Table 1. – Frequencies of the moss species in the samples collected in particular regions.

Region/species	Total	*Hamatocaulis vernicosus*	*Scorpidium cossonii*	*Warnstorfia exannulata*
Bohemian Massif	478	76 (15.9%)	42 (8.8%)	76 (15.9%)
West Carpathian	676	29 (4.3%)	220 (32.5%)	60 (8.9%)
Bulgarian Mts	483	24 (4.9 %)	6 (1.2%)	146 (30.2%)

Hedenäs & Kooijman (1996) stressed the importance of the concentration of iron in water in determining the distribution of *H. vernicosus*. In our study the iron content was not measured because of constraints on time and financial support. Iron concentration fluctuates widely in time (e.g., Hájek & Hekera 2004) and it is impossible to monitor it in such an extensive study. However, results from the Czech Republic show that the occurrence of *H. vernicosus* is not obligately associated with high iron content (Štechová & Kučera 2007).

The nomenclature follows Kubát et al. (2002) and Kučera & Váňa (2003). Nomenclature of S European vascular plants not in Kubát et al. (2002) follows Andreev et al. (1992).

Data analysis

For all the species at each location, the probability of their occurrence was analysed with respect to pH, ln-transformed conductivity and Ellenberg indicator values using a logistic regression fitted using Huisman-Olff-Fresco models (HOF; Huisman et al. 1993). HOF is a hierarchical set of five species response models, which increase in complexity: model I – flat with no response, II – monotonously increasing or decreasing, III – monotonously increasing or decreasing with a 'plateau', IV – symmetric unimodal and V – asymmetric unimodal response. For these models, four parameters were estimated, which was done using a non-linear maximum likelihood estimation procedure (Oksanen & Minchin 2002). This routine was run externally from the JUICE program (Tichý 2002) using a procedure developed by David Zelený and Lubomír Tichý and available at http://botanika.bf.jcu.cz/david/hof.php. Ten outlying conductivity values for salt-rich travertine fens (2000–10,000 $\mu S.cm^{-1}$) were not included in the analysis as they strongly influenced the shapes of the species response curves. Only one sample from these high-conductivity fens contained some plants of one of the study species (*S. cossonii*). For each species the response optimum, defined as that part of the gradient where the predicted probability of occurrence was highest, and the response interval (i.e., ecological amplitude), defined as the distance between parts of the gradient where the predicted probability of occurrence reached more than half of that of the maximum predicted probability of occurrence, were determined.

At each location, the vascular plants and bryophytes that had similar habitat requirements to the target species were determined by calculating the inter-specific associations of the species. The phi-coefficient has was used as a measure of species fidelity (Chytrý et al. 2002).

Results

Frequency of target species

The number of samples containing particular target species differs across locations (Table 1). The highest frequency of *Hamatocaulis vernicosus* was recorded in BM, while that of *Scorpidium cossonii* was highest in WC, where this species occurred in one third of the samples. In contrast, the frequency of *S. cossonii* in the Bulgarian samples was very low; this species was recorded only in six samples at three recently discovered localities. *Warnstorfia exannulata* occurred most frequently in the Bulgarian mountains, especially above the timberline.

Habitat requirements of target species

Response curves of the species to pH, conductivity, Ellenberg moisture and nutrient indicator values showed a high level of niche differentiation within the species group, which is consistent across regions (Fig. 1, Table 2). While ecological requirements clearly differed among the species within each region, the species optima and amplitudes were shifted between regions in several cases.

Diversification of the realized niches along the pH gradient of the species studied was clear. *Warnstorfia exannulata* preferred slightly acid conditions, about pH 5.6 at all the locations studied. *Scorpidium cossonii* represented the other extreme, with a monotonic response curve peaking at the alkaline end of the gradient at all locations. Its optimum revealed by the HOF method corresponded to the maximum pH value in the data set. The position of realized niche of *Hamatocaulis vernicosus* was intermediate. Response optimum of *H. vernicosus* on the pH gradient varied in the different areas, from pH 6.0 in Bulgaria, which is close to the optimum of *W. exannulata*, to pH 6.7–7.0 in WC and BM, which is close to the optimum of *S. cossonii*. The patterns in species niche diversification with respect to conductivity (Fig. 1) were similar to those with respect to pH, with the exception of Bulgarian data set in which the realized niche of *H. vernicosus* was better differentiated from that of *S. cossonii* than at the two other locations studied.

The species realized niches differed not only in terms of pH and conductivity, but also in terms of Ellenberg's moisture and nutrients (Fig. 1). *Warnstorfia exannulata* occurred in wetter habitats than the other two species at both the BG and BM localities, but not in WC. *Hamatocaulis vernicosus* and *S. cossonii* had roughly the same moisture demands. *Warnstorfia exannulata* was tolerant of a wide range of Ellenberg's nutrients at all locations, but its optimum shifted towards less mineral- and more nutrient-rich habitats in WC. The optimum of *S. cossonii* was in nutrient-poorer habitats that of *H. vernicosus*.

Inter-specific co-occurrences

Association of other bryophyte species with particular target species confirmed the ecological requirements indicated by the environmental variables (Table 3). The species composition of the vegetation harbouring target species varied according to the species and region. Of the potential competitors of *H. vernicosus*, *Calliergonella cuspidata* was strongly associated with this species in both BM and BG mires. As regards *Sphagnum* species, the vegetation affinities of *H. vernicosus* were similar to those of *Sphagnum teres* in BM and that of *S. contortum* in BG. In WC, this species was not strongly associated with any

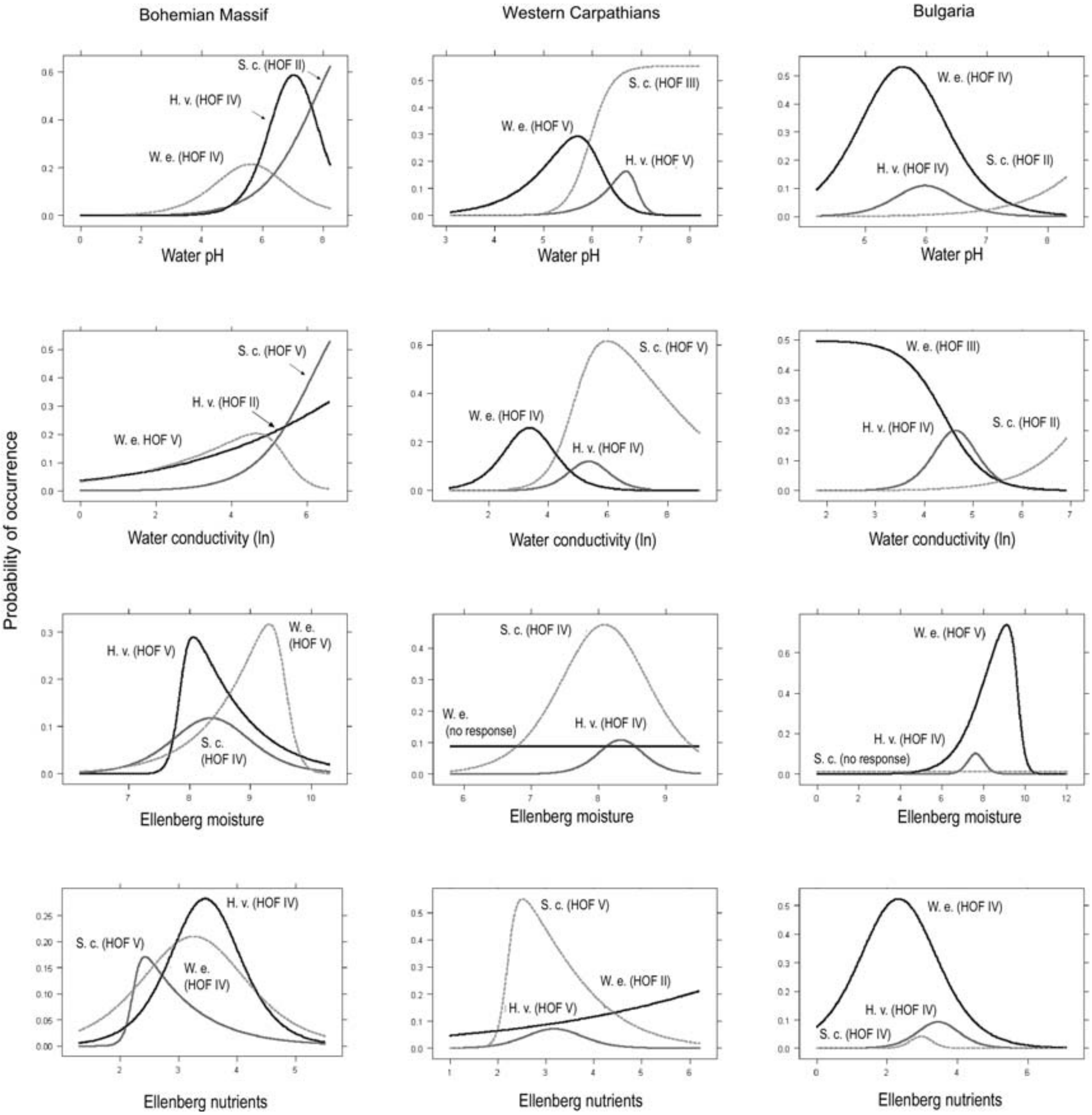

Fig. 1. – Species response curves, in terms of water pH, water conductivity (ln-transformed), and Ellenberg moisture and nutrient indicator values obtained by using logistic regression and HOF models, for the different regions studied. H.v. – *Hamatocaulis vernicosus*, S.c. – *Scorpidium cossonii*, W.e. – *Warnstorfia exannulata*.

Sphagnum species. At all three regions, *H. vernicosus* was positively associated with vascular plant species with a boreal and boreo-continental distribution, which are considered to be glacial relicts in Central and SE Europe, namely *Menyanthes trifoliata* (BM, WC), *Carex diandra* (BM), *C. lasiocarpa* (WC), *C. chordorrhiza* (WC), *C. dioica* (WC) and *C. buxbaumii* s.s. (BG). In Bulgaria, *H. vernicosus* was strongly positively associated also with grass and herb species typical of managed fen grasslands in SE Europe (e.g., *Holcus lanatus*, *Myosotis sicula*, *Oenanthe banatica*).

Table 2. – Optima and amplitudes (in parentheses) of habitat parameters of the mosses obtained by using the HOF models. Cond – conductivity; Moist – Ellenberg moisture; Nutr – Ellenberg nutrients. Conductivity optimum and amplitude were calculated from ln-transformed values. Optima are presented as untransformed values, whereas amplitudes are presented on a ln-scale (*). Ellenberg indicator values were calculated as unweighted mean from all vascular plant species present in the vegetation plot.

	Bohemian Massif				West Carpathians				Bulgarian Mountains			
	pH	Cond	Moist	Nutr	pH	Cond	Moist	Nutr	pH	Cond	Moist	Nutr
Hamatocaulis vernicosus	7.03	736	8.06	3.45	6.68	211	8.32	3.17	5.98	103	7.63	3.45
	(1.94)	(2.36*)	(0.96)	(1.42)	(0.72)	(1.61*)	(0.79)	(1.42)	(1.18)	(1.07*)	(0.91)	(1.41)
Scorpidium cossonii	8.23	736	8.35	2.42	8.20	392	8.08	2.51	8.30	993	6.00	2.97
	(1.17)	(1.02*)	(1.52)	(0.92)	(2.26)	(3.74*)	(1.57)	(1.44)	(0.53)	(0.58*)	(12.00)	(0.74)
Warnstorfia exannulata	5.60	106	9.31	3.26	5.69	29	7.65	6.20	5.61	6	9.12	2.33
	(2.81)	(2.89*)	(1.00)	(2.10)	(1.42)	(2.04*)	(3.70)	(2.54)	(1.70)	(2.61*)	(1.96)	(2.58)

Table 3. – Species which are positively associated with the moss species in particular regions. The number in parenthesis is the value of phi-coefficient indicating the strength of the inter-specific association between the species studied and other species in the data set.

Species studied	Czech Republic	West Carpathian	Bulgaria
Hamatocaulis vernicosus	*Calliergonella cuspidata* (56.6)	*Carex lasiocarpa* (41.4)	*Sphagnum contortum* (34.1)
	Bryum pseudotriquetrum (56.4)	*Tomentypnum nitens* (29.5)	*Calliergonella cuspidata* (33.6)
	Equisetum fluviatile (55.3)	*Salix pentandra* (29.2)	*Philonotis caespitosa* (33.5)
	Menyanthes trifoliata (43.3)	*Galium uliginosum* (28.0)	*Myosotis sicula* (30.9)
	Carex diandra (41.7)	*Carex chordorrhiza* (25.7)	*Holcus lanatus* (29.5)
	Campylium stellatum (41.6)	*Menyanthes trifoliata* (24.6)	*Galium palustre* (28.7)
	Sphagnum teres (38.4)	*Valeriana simplicifolia* (23.1)	*Carex buxbaumii* s.s. (28.2)
	Valeriana dioica (35.3)	*Riccardia multifida* (21.4)	*Plagiomnium affine* agg. (27.4)
	Drepanocladus polygamus (31.5)	*Carex dioica* (18.2)	*Veronica scutellata* (27.2)
	Calliergon giganteum (31.2)	*Crepis paludosa* (18.3)	*Oenanthe banatica* (25.1)
Scorpidium cossonii	*Campylium stellatum* (58.8)	*Campylium stellatum* (58.5)	*Carex lepidocarpa* (32.6)
	Eriophorum latifolium (47.9)	*Eleocharis quinqueflora* (54.2)	*Dactylorhiza incarnata* (32.5)
	Carex panicea (46.0)	*Carex davalliana* (53.4)	*Eleocharis quinqueflora* (31.0)
	Parnassia palustris (43.6)	*Pinguicula vulgaris* (52.7)	*Eleocharis uniglumis* (29.2)
	Fissidens adianthoides (43.5)	*Eriophorum latifolium* (50. 0)	*Epilobium parviflorum* (26.6)
	Juncus alpinoarticuslatus (41.4)	*Bryum pseudotriquetrum* (49.5)	*Blysmus compressus* (24.6)
	Eleocharis quinqueflora (39.6)	*Parnassia palustris* (45.4)	*Linum catharticum* (24.1)
	Trichophorum alpinum (38.0)	*Primula farinosa* (43.7)	*Carex panicea* (22.2)
	Carex demissa (36.8)	*Carex panicea* (42.8)	*Ononis arvensis* (22.2)
	Linum catharticum (36.8)	*Equisetum palustre* (41.1)	*Philonotis calcarea* (22.2)
Warnstorfia exannulata	*Sphagnum subsecundum* (30.1)	*Sphagnum subnitens* (27.6)	*Carex nigra* (43.3)
	Drepanocladus polygamus (27.7)	*Lotus pedunculatus* (27.3)	*Sphagnum platyphyllum* (32.4)
	Carex elata (24.9)	*Sphagnum contortum* (27.1)	*Primula farinosa* s. *exigua* (32.4)
	Potentilla palustris (23.0)	*Viola palustris* (26.6)	*Sphagnum subsecundum* (32.3)
	Calliergon giganteum (21.8)	*Juncus bulbosus* (24.7)	*Scapania irrigua* (31.7)
	Lysimachia thyrsiflora (21.4)	*Carex demissa* (23.1)	*Nardus stricta* (31.5)
	Sphagnum obtusum (18.5)	*Sphagnum flexuosum* (22.9)	*Philonotis seriata* (30.6)
	Sphagnum fimbriatum (17.8)	*Carex canescens* (21.7)	*Pinguicula balcanica* (30.3)
	Calamagrostis canescens (17.6)	*Sphagnum squarrosum* (21.6)	*Warnstorfia sarmentosa* (26.1)
	Peucedanum palustre (17.4)	*Drosera rotundifolia* (20.8)	*Juncus filiformis* (25.8)

Species, which were strongly associated with *Scorpidium cossonii*, represent mostly a geographically rather uniform group of strongly calcium-tolerant species of low-productive habitats (*Campylium stellatum*, *Eriophorum latifolium*, *Carex panicea* and *Eleocharis quinqueflora*). Although the species associated with *W. exannulata* varied considerably among the regions studied, they were mostly species typical of poor and moderately rich fens, which lack calcium-tolerant species (e.g., *Carex canescens*, *Juncus filiformis*, *Lysimachia thyrsiflora*, *Potentilla palustris*, *Sphagnum flexuosum* and *S. subsecundum*). In WC and BG, the species of sub-alpine springs (e.g., *Carex lachenalii*, *Philonotis seriata*, *Primula farinosa* subsp. *exigua*, *Sphagnum platyphyllum*, *Swertia perennis*, *Warnstorfia sarmentosa*) also showed a positive association with *W. exannulata*.

Discussion

Niche diversification

Comparison of species response curves, response optima and amplitudes with respect to pH and conductivity showed that our working hypothesis of different optima for a species in different regions holds only for *H. vernicosus*, which occupies the middle of both the pH and conductivity gradients. Ecological behaviour of two other species (*W. exannulata*, *S. cossonii*) was very similar at all the locations. In Bulgaria, *H. vernicosus* occupied slightly acidic habitats and showed a wider ecological amplitude with respect to pH. A possible explanation for this is the ecotypic adaptation of local populations caused by differences in the histories of the localities, i.e. distribution of refugia with respect to substrate acidity (Hájková et al. 2008). Pleniglacial refugia for mire flora are found mostly on crystalline bedrocks in Bulgaria and are rather acidic for that reason. On the other hand, the refugia in the West Carpathians are often alkaline (Hájek et al. 2007, Horsák et al. 2007). A shift in ecological optimum towards acidic conditions is recorded for other bryophytes in Bulgaria, especially *Sphagnum warnstorfii*, *S. teres* (Hájková & Hájek 2007) and *Aulacomnium palustre* (Hájková et al. 2008). However, a change in competitive regimes can contribute to a wider realized niche as shown by *H. vernicosus* in Bulgaria, where *S. cossonii* is extremely rare and *W. exannulata* is confined to the highest altitudes. This pattern can be regarded as a sign of competitive release, i.e. extension of the species ecological amplitude in the absence of a potential competitor (Coudun & Gégout 2005). We assume there is a potential for competition between the species studied at the landscape level due to niche overlap between *H. vernicosus* and the other two species (Štechová & Kučera 2007). Although bryophytes can tolerate low resource levels, they compete intensely with each other. There is abundant evidence from community structure and transplantation experiments that competitive hierarchies among bryophytes exist, with well-adapted species superior to widespread ones in specific environments (see Rydin 1997 for review). At some of the localities studied, many small fens are dominated by one species (*S. cossonii*, *H. vernicosus*, *W. exannulata*) and the other two species are absent, even when habitat conditions appear to be favourable. On the other hand, the mosses studied often grew together not only in the vegetation plot, but also in mixed clumps at other localities (e.g., Třeboňská pánev basin in the Bohemian Massif). Future research should focus on addressing questions under which conditions competitive exclusion occurs within the group of species studied.

Comparison of our results with those published on the habitat preferences of the species studied is not straightforward, because the latter are mostly presented in terms of the minimum, maximum and mean/median values of particular measurements. These values may reflect differences in the commonness of particular habitats among regions and possible stochastic occurrences of the species in sub-optimal conditions, even when the species are in fact ecologically similar at all the locations (e.g., Hájková et al. 2007). All our measurements of pH and conductivity in the habitats of *H. vernicosus* fall within the range reported from Scandinavia (pH 5.4–7.8 and conductivity 16–396 $\mu S.cm^{-1}$; Hedenäs 2003). Mean values reported from Scandinavia (Hedenäs & Kooijman 1996, Hedenäs & Eldenäs 2007) are close to the optima of *H. vernicosus* in Bulgaria.

Concerning *W. exannulata*, the optimal pH value was similar at all locations and varied only between 5.6 and 5.7. However, the realized niche of this species is wide as it can tolerate higher pH levels. A wide realized niche of *W. exannulata* was reported long ago, e.g. by Limpricht (1904), who described many varieties of this species (Limpricht 1904). Likewise, the controversial reports on the ecological requirement of *W. exannulata* in modern ecological literature may reflect the wide realized niche of this species. Results originating from different geographical location or climatic conditions (Jannsens 1983, Ilyashuk 2002, Szankowski & Klosowski 2004) indicate acidophilous behaviour of this species, while the study of Hedenäs (2003) characterized *W. exannulata* as a species typical of intermediate mineral-rich environments.

Niche diversification in this group of species along the base saturation gradient coincides partially with nutrient availability, approximated by the Ellenberg indicator values of the co-occurring vascular plants. *Scorpidium cossonii* performed optimally in nutrient-poorer habitats than *H. vernicosus* in all three locations. The former species occurs frequently in base-richest tufa-forming fens, which are very poor in phospohorus, whereas the latter prefers extremely rich fens that are not phosphorus-limited (Rozbrojová & Hájek 2008). In the Bohemian Massif, many fens harbouring *H. vernicosus* occur at fishpond margins that are eutrophicated by pond water rich in phosphorus. In contrast, *S. cossonii* is, even in the same mire complex, confined to spring fens that are fed by groundwater poor in phosphates and ammonium (Navrátilová et al. 2006).

Other aspects of Hamatocaulis vernicosus distribution

The next factor that shapes the distribution of this study group of species is the relic character of the *H. vernicosus* localities, which is indicated by the frequent co-occurrence of boreal sedges. This is supported by the fact that *H. vernicosus* is common in the regions where there are relic mires, but absent where the mires are young. This species was extremely rare, and currently is extinct at the Beskydy Mts (NW margin of the Carpathians), where mires developed after extensive deforestation during the largest Walachian colonization, which occurred 600–700 years ago (Rybníčková et al. 2005), but rather common in the neighbouring Orava region where fens have a long history (e.g., Rybníček & Rybníčková 2003, Horsák et al. 2007). Recent colonization of new areas is not assumed, because the dispersal ability of *H. vernicosus* is very poor in Central and SE Europe. During our study, sporophytes were observed only a few times in field and only once in herbaria.

Besides relic species, *H. vernicosus* often co-occurs with the ubiquitous wetland species *Calliergonella cuspidata* (see also Church et al. 2001 and Müller & Bauman 2004), which is competitively stronger than fen moss specialists when the nutrient supply is increased (Kooijman 1993) and can benefit also from the increased shading that results from the enhanced growth of vascular plants (e.g., van der Hoeven et al. 1993). As the distribution of rare species of bryophytes is often a product of a trade-off between the probability of colonizing new habitats and the establishment in the presence of competitors (Hutsemekers et al. 2008), the low dispersal ability of *H. vernicosus* combined with frequent co-occurrence with competitively superior species seems to be the crucial factors determining its rarity and threatened status in Central and S Europe. Further conservation monitoring should therefore focus on the inter-specific interactions between *H. vernicosus* and its potential competitors at localities with different nutrient inputs.

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Souhrn

Článek se zabývá studiem ekologických nároků a mezidruhových vazeb tří blízce příbuzných bokoplodých slatiništních mechů v odlišných částech Evropy (Český masiv, Západní Karpaty a Bulharsko). Největší pozornost je věnována druhu *Hamatocaulis vernicosus*, který je považován za celoevropsky ohrožený mech a je sledován v rámci programu Natura 2000. Dalšími studovanými druhy jsou *Scorpidium cossonii* a *Warnstorfia exannulata*, které podobně jako první druh často tvoří dominantu v různých typech rašeliništních biotopů a představují tak jeho potenciální kompetitory. Ve srovnání s podobnými studiemi ze severní Evropy jsme k posouzení diverzifikace nik mezi sledovanými druhy použili křivky druhových odpovědí na gradienty prostředí (HOF modely), kde do analýzy vstupují i údaje ze slatinišť, kde se zájmové druhy nevyskytují.

Srovnání mezi regiony ukázalo, že *Hamatocaulis vernicosus* má větší zastoupení než *Scorpidium cossonii* ve fytocenologických snímcích pocházejících z oblasti Českého masivu a Bulharska, zatímco *Scorpidium cossonii* se nejčastěji vyskytuje ve snímcích ze Západních Karpat. *Warnstorfia exannulata* je dosti častá v Českém masivu a v Bulharsku, kde je však vázána jen na nejvyšší polohy.

Na základě výsledků HOF modelů lze říci, že *Warnstorfia exannulata* má ve všech studovaných oblastech širokou realizovanou niku, preferuje však spíše kyselá stanoviště s pH kolem 5.6, zatímco *Scorpidium cossonii* vyhledává biotopy s nejvyšším obsahem bází (pH vyšší než 7). Optimální pH pro výskyt druhu *Hamatocaulis vernicosus* se pohybuje v rozmezí 6 až 7 v závislosti na regionu. Tento posun ve stanovištních nárocích lze vysvětlit jak lokální adaptací místních populací na různé úrovně pH v závislosti na historické četnosti jednotlivých biotopů v krajině, tak i kompetičními vztahy měnícími se s četností jednotlivých druhů. Srovnání dále ukázalo, že *Warnstorfia exannulata* roste spíše na stanovištích s vyšší hladinou podzemní vody a má větší toleranci vůči zvýšenému obsahu živin. Produktivita stanoviště se podílí i na diverzifikaci nik druhů *Hamatocaulis vernicosus* a *Scorpidium cossonii*. Výsledky HOF modelů byly potvrzeny i stanovením druhů s vysokou mírou věrnosti (fidelity) ke studovaným druhům. Tato analýza navíc ukázala vazbu druhu *Hamatocaulis vernicosus* na biotopy s výskytem boreálních druhů ostřic, které jsou ve studovaných oblastech považovány za reliktní. Zjištěné výsledky mohou pomoci při výběru lokalit ohroženého druhu *Hamatocaulis vernicosus* tak, aby se druh chránil v prostředí, na které je v daném území dobře adaptován.

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