Preslia 83: 1–24, 2011

Alpine wetlands in the West Carpathians: vegetation survey and vegetation–environment relationships

Vysokohorská mokřadní vegetace v Západních Karpatech: vegetační přehled a vztahy vegetace a prostředí

Lucia Sekulová[1], Michal Hájek[1,2], Petra Hájková[1,2], Eva Mikulášková[1] & Zuzana Rozbrojová[1,2]

[1]*Department of Botany, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic, e-mail: sekulova@sci.muni.cz, hajek@sci.muni.cz, buriana@sci.muni.cz, evamikul@gmail.com, zuzkaroz@sci.muni.cz;* [2]*Department of Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Lidická 25/27, CZ-657 20 Brno, Czech Republic*

Sekulová L., Hájek M., Hájková P., Mikulášková E. & Rozbrojová Z. (2011): Alpine wetlands in the West Carpathians: vegetation survey and vegetation–environment relationships. – Preslia 83: 1–24.

Wetland vegetation in the sub(alpine) zone of the West Carpathians (Poland, Slovakia) was studied with particular reference to the following questions: (i) What are the main types of (sub)alpine fen, bog and spring vegetation above the timberline in the West Carpathians? (ii) Which major environmental gradients are associated with the variation in floristic composition? (iii) What determines the α-diversity of bryophytes and vascular plants in the different vegetation types? Vegetation plots were sampled and direct measurements of certain environmental characteristics recorded. Cluster analysis was used to distinguish the vegetation types, DCA and CCA to reveal the main vegetation gradients and environmental factors, and general regression models to identify the factors determining the α-diversity. Classification at the level of 12 clusters was ecologically and syntaxonomically interpretable. Two associations not mentioned in the most recent vegetation survey of Slovakia were distinguished and the syntaxonomical positions of others revised. The synthesis of collected and published vegetation data for the two countries has modified the classification concept of (sub)alpine wetlands in the West Carpathians. Whereas pH predominantly determined floristic differences among classes, different factors governed the species composition within classes. While the diversity of the vegetation of springs (*Montio-Cardaminetea*) was mostly determined by water chemistry, altitude and geomorphology appeared to be more important within fens and bogs. The species richness of spring vegetation was more influenced by mineral richness than water pH and for bryophyte richness the slope inclination was also important. The species richness of fens and bogs increased with pH. It is concluded that the ecological gradients influencing the floristic composition and species richness of (sub)alpine wetlands are strongly habitat-dependent.

Keywords: azonal habitats, bogs, environmental gradients, fens, species richness, springs, water chemistry

Introduction

Wetlands are important in terms of their biodiversity and need of protection, but are one of the most threatened habitats in all of Europe. Precise knowledge of the factors that are important in the development of particular plant communities is a good basis for justifying appropriate conservation management. Water pH and mineral richness are well known major determinants of floristic variation in wetland vegetation (Bragazza & Gerdol 2002, Sjörs & Gunnarsson 2002, Nekola 2004, Hájek et al. 2006, Hájková et al. 2008, Strohbach et al. 2009, Lamentowicz et al. 2010, Tichý et al. 2010). Most of the above studies focused on mire or wet grassland vegetation below the timberline. However, some studies indicate that factors determining the diversity of wetlands might differ above and below the timberline (Hájková et al. 2006). Therefore, it would be worth focusing on the alpine ranges and analysing them separately. In general, there is very little data on environmental gradients affecting the distribution patterns of plant communities in alpine ranges (Vonlanthen et al. 2006) and only a few studies on wetland vegetation ecology above the timberline (Molina 2001, Cooper et al. 2010, Lamentowicz et al. 2010). In recent years, arctic-alpine tundra vegetation has received more attention due to the increasing risk of accelerated climate change causing shifts in vegetation belts (e.g. Batllori et al. 2009, Britton et al. 2009, Wilson & Nilsson 2009) and the possibility of utilizing repeated vegetation mapping to indicate long-term climatic changes (Prach et al. 2010). In order to extend this research to alpine wetlands, thorough vegetation surveys are needed. Phytosociology has, however, traditionally been based on local studies of relatively small areas (Ewald 2003), which make broad-scale comparisons complicated. Specific broad-scale vegetation surveys of alpine wetlands have most often concerned only a part of wetland vegetation, e.g. springs (Molina 2001) or peatland (Cooper et al. 2010) or have dealt only with rather rough high-rank syntaxa (Zechmeister & Mucina 1994), usually without measuring any environmental variables (but see Hájková et al. 2006 for Bulgaria).

Despite the uniqueness of alpine wetland habitats, they have received little attention in the West Carpathians. Studies of mire and spring vegetation in the West Carpathians have focused on the overall floristic composition of the vegetation (Hadač 1983, Rybníček et al. 1984, Valachovič 2001), altitudinal changes (Valachovič & Janovicová 1999) and responses of plants to ecological gradients (e.g. Hájek 2002, Hájek et al. 2002, Hájková & Hájek 2004, Hájková et al. 2004), or wetlands were studied as part of a research project in a particular area (Szafer et al. 1923, Pawlowski et al. 1928, Krajina 1933, Sillinger 1933, Hadač 1956, Hadač et al. 1969a, Kliment et al. 2008). In general, the majority of the studies on vegetation–environment relationships are conducted below the timberline, whereas subalpine and alpine wetlands are studied from a purely floristic or phytosociological point of view and there is no synthesis of the ecological data that has been measured.

A comprehensive collection of phytosociological data on springs and mires is surprisingly inadequately supplemented by directly measured ecological data. Moreover, the occurrence of many critical taxa in the bryophyte layer has meant that the majority of phytosociological data lacks a complete inventory of the bryophyte layer, which is particularly important in wetland communities. This study is based predominantly on data of a detailed investigation of both bryophytes and vascular plants, sampled in two countries (Slovakia, Poland) plus directly measured physical-chemical properties of the water. The data was used to address the following questions: (i) What are the main types of (sub)alpine fen, bog and spring vegetation above the timberline in the West Carpathians? (ii) Which major environmental gradients are associated with the variation in the floristic composition of the vegetation? (iii) What determines the α-diversity of bryophytes and vascular plants in different vegetation types?

Material and methods

Study area

Mountain ranges exceeding 1700 m a.s.l. in the West Carpathians were studied (Fig. 1): Vysoké Tatry Mts (2654 m), Západné Tatry Mts (2248 m), Belianske Tatry Mts (2152 m), Nízke Tatry Mts (2043 m) and Malá Fatra Mts (1709 m). The highest parts of the West Carpathians were strongly influenced by a Pleistocene glacier, mostly in the northern parts, where there are a large number of glacial lakes. A variety of wetlands can be found in such areas. In the lower mountains subalpine wetland habitats develop only in small areas around springs.

With the exception of the eastern part of the Nízke Tatry Mts, the bedrock of the mountains is crystalline and mostly consists of granite, granodiorite and gneiss. Mostly haplic to humic podzolic soils are present at altitudes above 1500 m a.s.l. (Šály & Šurina 2002). At lower altitudes a nappe consisting of limestone and shale can be found. However, due to the local occurrence of metamorphosed basic rocks there are some basic soils. The eastern part of the Nízke Tatry Mts consists of gneisses (Lexa et al. 2000). The climate is cold and humid, with short, wet summers and cold winters with heavy snow accumulation, which provides protection from deep soil frosts. The mean precipitation is more than 1200 mm and the mean annual temperature is approximately 0 °C. The local climate varies considerably and is affected by the orientation of the valleys.

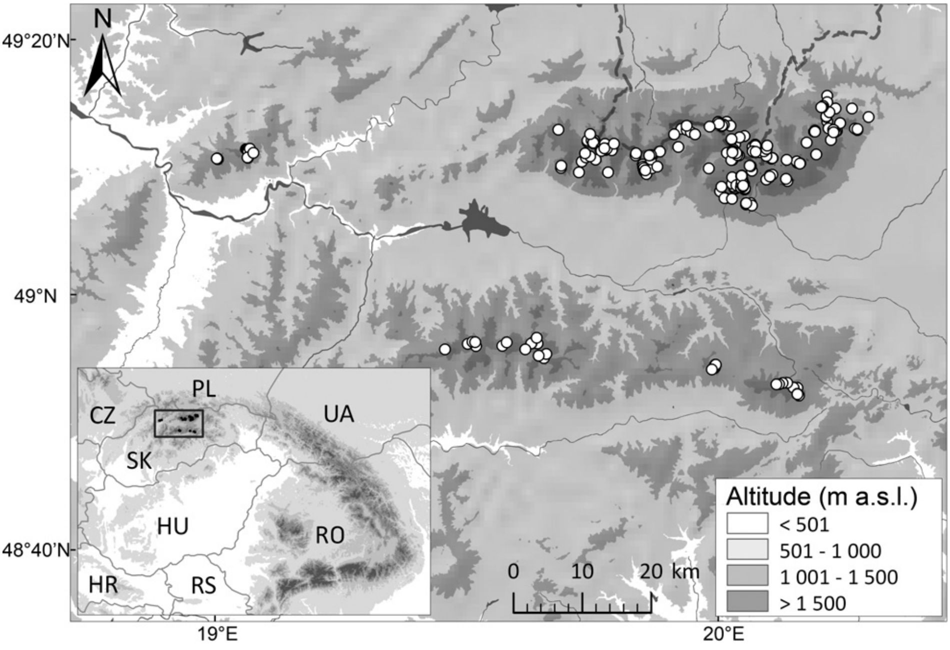


Fig. 1. – The location of the sites studied in the Western Carpathians. The coordinates presented were obtained using the WGS 84 system.

Data collection

The basic data (450 vegetation plots) was that of vegetation plots (250) sampled for this study plus an additional 200 plots from the Central Database of Phytosociological Relevés in Slovakia (Hegedüšová 2007). Vegetation plots (4 × 4 m) at all the springs, bogs and fens above the timberline (approximately 1500 m a.s.l.) in the study area were sampled during the vegetation seasons of 2005–2009. Smaller plot sizes (1–15 m^2) were used for patches of vegetation that were too small to sample using 16 m^2 plots. If possible, all wetland vegetation and habitat types were included. Within each vegetation plot the following environmental variables were recorded: water pH, conductivity, altitude, slope inclination and shape of the valley (1: narrow, V-shaped; 2: wider V-shaped; 3: wide U-shaped; 4: very wide, U-shaped with glacial lakes). The pH and conductivity were measured in situ directly in the water. If the water table was below the surface a small shallow pit was dug and the water was allowed to clear before the measurements were recorded. Both factors were standardized to 20 °C. Conductivity caused by protons was subtracted in acidic waters with a $pH < 5.5$ (Sjörs 1952). The corrected conductivity was used as a proxy of total mineral richness in the water sample, as it is strongly correlated with the sum of the concentrations of calcium and magnesium (Malmer 1986, Sjörs & Gunnarsson 2002, Hájek & Hekera 2004). All vascular plants and bryophytes were identified and their cover was estimated using a nine-grade cover scale (Barkmann et al. 1964). The nomenclature of the taxa follows the Checklist of non-vascular and vascular plants of Slovakia (Marhold & Hindák 1998).

Data processing

All of the 450 vegetation plots from the (sub)alpine belt of the entire West Carpathians were classified. The types of vegetation were distinguished by means of cluster analysis in PC-ORD software (Grandin 2006), using Ward's method, with Euclidean distance as a resemblance measure; species cover was replaced by percentages and logarithmically transformed. In this classification, 12 clusters were accepted at the highest level of the hierarchy. Diagnostic species for these clusters were determined a posteriori, using the Φ coefficient of association standardized to equal group size (Tichý & Chytrý 2006) by calculating the fidelity of each species to each cluster in the program JUICE (version 7.0, www.sci.muni.cz/botany/juice). The threshold value required for a species to be considered as diagnostic was set to $\Phi \geq 0.30$. Only species with a significance $P < 0.05$ in the Fisher exact tests were included. The results of the classification were summarized in a synoptic table. The diagnostic species were ranked by decreasing fidelity. Box plots of mean measured factors (water pH, corrected conductivity, altitude) and the Ellenberg indicator value for nutrient availability (Ellenberg et al. 1992) were used to describe particular types of vegetation. The Tukey post-hoc test was used following one-way ANOVA for multiple comparisons of the particular groups. The groups were further described and interpreted syntaxonomically and named according to the rules of the International Code of Phytosociological Nomenclature (Weber et al. 2000). In the text, § means the Article of the Code.

Since using published data on water pH is not recommended due to the different sampling protocols used (Tahvanainen & Tuomaala 2003), only plots for which pH and conductivity were measured in this study were included in the ecological analyses (250 plots). Major gradients in floristic composition were analysed using the Detrended Correspondence Analysis (DCA) in the CANOCO package (version 4.5, Biometris, Wageningen, České Budějovice). In these analyses the cover values in percentages were square-root transformed and rare species were downweighted. For ecological interpretation of the ordination axes, environmental variables were plotted onto a DCA ordination diagram as supplementary variables and a correlation matrix using the Pearson correlation coefficient, created in the STATISTICA program (version 9.0, StatSoft Inc., Tulsa) using environmental variables and ordination scores on the axes for the entire dataset and three subsets: spring (*Montio-Cardaminetea* class), fen (*Scheuchzerio-Caricetea nigrae* class) and bog (*Oxycocco-Sphagnetea* class).

The vegetation samples were further subjected to canonical correspondence analysis (CCA), in which the environmental variables were explanatory variables. The aim was to find the best predictors of floristic composition using the forward selection procedure. The significance of each potential predictor of the environmental variables was calculated using a partial Monte Carlo test and only predictors with a significance of $P < 0.05$ were included in the CCA model.

Since the vegetation plots were unequal in size, which might have influenced the results on species richness (but species counts showed no relationship with plot size), and the environmental factors are not correlated with plot size, the effect of unequal plot sizes was removed by calculating linear regressions of the local species richness on log-transformed plot size (Chytrý et al. 2003). Logarithmic transformation was used in order to fit the empirical species–area relationship (Rosenzweig 1995). In the analyses, corrected α-diversity was obtained from the standardized residuals of this regression instead of species counts.

To determine how plant species richness is related to environmental factors, general regression models were calculated (linear or quadratic) for all three main vegetation classes (springs, fens, bogs) using the STATISTICA program. The models were tested using partitioning sums of squares and the model providing the best fit was used.

Results

Diversity of vegetation

Numerical classification reproduced some of the traditional expert-based phytosociological associations at the level of 12 groups. With the exception of bog hollow vegetation (*Sphagnion cuspidati* alliance) represented by two associations in one group, all types can be regarded as associations (for diagnostic species see Table 1 and for environmental variables see Fig. 2). Four of them represent bog vegetation with peat accumulation (*Oxycocco-Sphagnetea* class), three fen vegetation (*Scheuchzerio-Caricetea nigrae* class) and four the vegetation of springs (*Montio-Cardaminetea* class).

Syntaxonomical synopsis of the types of vegetation recognized in this study:

- *Oxycocco-Sphagnetea* Br.-Bl. et Tüxen ex Westhoff et al. 1946
  - *Sphagnetalia magellanici* Kästner et Flößner 1933
    - *Oxycocco microcarpi-Empetrion hermaphroditi* Nordhagen ex Du Rietz 1954
      - *Trichophoro cespitosi-Sphagnetum compacti* Warén 1926
      - *Carici lachenalii-Eriophoretum vaginati* (Krajina 1933) Šoltés in Valachovič et al. 2001
      - *Empetro nigri-Sphagnetum fusci* Osvald 1923
      - *Sphagno capillifolii-Caricetum canescentis* Hadač 1969

Scheuchzerio palustris-Caricetea nigrae Tüxen 1937
    Caricetalia nigrae Koch 1926
        Caricion canescenti-nigrae Nordhagen 1937
            Drepanocladetum exannulati Krajina 1933
            Calliergo sarmentosi-Eriophoretum angustifolii Hadač et Váňa 1967
    Scheuchzerietalia palustris Nordhagen 1937
        Sphagnion cuspidati Krajina 1933
            Carici rostratae-Drepanocladetum fluitantis Hadač et Váňa 1967
            Drepanoclado fluitantis-Caricetum limosae (Kästner et Flössner 1933) Krisai 1972

Montio-Cardaminetea Br.-Bl. et Tüxen ex Klika et Hadač 1944
    Montio-Cardaminetalia Pawłowski in Pawłowski et al. 1928
        Dichodontio palustris-Swertion perennis Hadač 1983
            Calthetum laetae Krajina 1933
            Caltho-Dicranelletum squarrosae Hadač 1956
            Crepido paludosae-Philonotidetum seriatae Hadač et Váňa 1972
            Cardaminetum opicii Szafer et al. 1923
        Cratoneurion commutati Koch 1928
        Cardamino opicii-Cratoneuretum falcati Szafer et Sokolowski 1927

Plant community characteristics and nomenclature

1. *Trichophoro cespitosi-Sphagnetum compacti* Warén 1926

Nomen conservandum propositum et nomen mutatum propositum
Orig. (Warén 1926): *Scirpus caespitosus-Sphagnum compactum*-Ass.
Syn.: *Trichophoretum austriaci* Zlatník 1928, *Trichophoro austriaci-Sphagnetum compacti* Krisai 1966, *Scirpetum austriaci* Osvald 1923 (§ 3d)

This boreal bog community is dominated by *Sphagnum compactum,* accompanied by *Carex pauciflora*, *Trichophorum cespitosum* and occassionally also by other species of bog vascular plants such as *Empetrum nigrum* agg., *Eriophorum vaginatum* and *Vaccinium uliginosum* agg. Some species that are typical of this community in northern Europe are not present (e.g. *Betula nana*, *Rubus chamaemorus* and *Sphagnum lindbergii*; Dierßen 1996). On the other hand, some species of the surrounding subalpine communities may occur because of the spatial mass effect (e.g. *Homogyne alpina, Nardus stricta, Campanula alpina* and *Ligusticum mutellina*).

This community is species-poor, with a mean number of 12 species, and is usually found on gentle slopes. The peat layer is 0.5–1 m thick (Šoltés et al. 2001) and in winter the community is covered by a deep layer of snow.

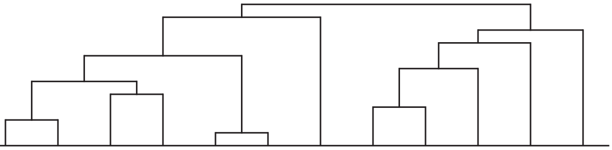
This community was recorded at an altitude of 1500–2100 m a.s.l. in the Vysoké Tatry Mts (both in Slovak and Polish part) and Západné Tatry Mts. The water pH was 3.6–5.4, and conductivity 5–47 $\mu S \cdot cm^{-1}$.

2. *Carici lachenalii-Eriophoretum vaginati* (Krajina 1933) Šoltés in Valachovič et al. 2001

Orig. (Valachovič et al. 2001): *Carici lachenalii-Eriophoretum vaginati* (Krajina 1933) Šoltés in Valachovič nom. nov. hoc loco)
Syn. *Eriophoretum vaginati tatricum* Krajina 1933 (§34)

This bog community is dominated by bryophytes (*Sphagnum compactum*, *S. palustre*, *S. capillifolium*, *S. girgensohnii*) and *Eriophorum vaginatum*. The vegetation is further enriched by hemicryptophytes from the neighbouring vegetation (e.g. *Carex lachenalii*,

Table 1. – Shortened synoptic table and dendrogram produced by cluster analysis. Presented values are percentage constancies with fidelity in upper index. Diagnostic species of particular associations defined by fidelity values (Φ ≥ 0.30*, Φ ≥ 0.40**) are ranked by decreasing fidelities in each column. The species with negative fidelity values and non significant fidelity values (Fisher's exact test P < 0.05) are not shown.



Group number	1	2	3	4	5	6	7	8	9	10	11	12
Number of vegetation plots	34	15	30	36	52	23	16	36	23	51	81	53
Average number of species	12	22	12	12	11	15	6	20	18	17	14	21
1. *Oxycocco-Sphagnetea*												
1.1. *Sphagnetalia magellanici*												
1.1.1. *Oxycocco microcarpi-Empetrion hermaphroditi*												
1.1.1.1. *Trichophoro cespitosi-Sphagnetum compacti*												
Sphagnum compactum	97**	27	23	22	.	.	.	.	.	.	.	.
Carex pauciflora	38**	.	.	.	.	.	13	.	.	.	.	.
Vaccinium myrtillus	53*	13	37	42	.	.	.	.	.	.	.	.
1.1.1.2. *Carici lachenalii-Eriophoretum vaginati*												
Campanula alpina	24	87**	.	.	.	.	.	.	.	.	.	.
Oreochloa disticha	9	47**	.	.	.	.	.	.	.	.	.	.
Carex atrata	.	47**	.	.	.	.	.	.	.	.	.	.
Carex lachenalii	.	60**	.	.	23	.	.	.	.	.	.	.
Hieracium alpinum agg.	12	53**	.	11	.	.	.	.	.	.	.	.
Lecidea limosa	.	27**	.	.	.	.	.	.	.	.	.	.
Avenula versicolor	.	27**	.	.	.	.	.	.	.	.	.	.
Agrostis rupestris	15	47**	.	.	.	.	.	.	.	.	.	.
Salix herbacea	.	40**	.	.	15	.	.	.	.	.	.	.
Festuca supina	.	27**	.	.	.	.	.	.	.	.	.	.
Dicranum groenlandicum	.	20**	.	.	.	.	.	.	.	.	.	.
Racomitrium lanuginosum	.	20**	.	.	.	.	.	.	.	.	.	.
Juncus trifidus	.	20**	.	.	.	.	.	.	.	.	.	.
Homogyne alpina	35	73**	.	42	10	26	13	14	.	.	.	.
Sphagnum palustre	.	47**	13	.	.	13	19	.	.	.	.	.
Soldanella carpatica	15	67*	.	11	12	13	.	22	35	.	.	26
Gentiana punctata	.	33*	.	.	.	.	.	.	.	.	.	.
Aulacomnium palustre	.	27*	.	.	8	.	.	.	.	.	.	.
Gentiana frigida	.	13*	.	.	.	.	.	.	.	.	.	.
Carex sempervirens	.	27*	.	.	.	.	.	.	.	.	.	13
Veratrum album subsp. *lobelianum*	21	47*	.	11	10	.	.	28	.	.	.	.
Polytrichum sexangulare	.	20*	.	.	6	.	.	.	.	.	.	.
Anthoxanthum alpinum	.	27*	.	.	.	.	.	.	.	8	.	.
Salix phylicifolia	.	13*	.	.	.	.	.	.	.	.	.	.
Oreogeum montanum	.	40*	.	.	.	.	.	11	22	.	.	.
Primula minima	.	27*	.	.	.	.	.	.	17	.	.	.
Conostomum tetragonum	.	13*	.	.	.	.	.	.	.	.	.	.
1.1.1.3. *Empetro nigri-sphagnetum fusci*												
Oxycoccus microcarpus	.	.	73**	.	.	.	.	.	.	.	.	.
Empetrum nigrum agg.	15	.	77**	.	.	.	13	.	.	.	.	.
Sphagnum magellanicum	26	.	87**	.	.	22	13	.	.	.	.	.
Sphagnum fuscum	15	.	60**	.	.	9	13	.	.	.	.	.
Sphagnum rubellum	12	13	63**	19	.	.	.	.	.	.	.	.
Vaccinium uliginosum agg.	12	.	53**	.	.	.	13	.	.	.	.	.

Group number	1	2	3	4	5	6	7	8	9	10	11	12
Number of vegetation plots	34	15	30	36	52	23	16	36	23	51	81	53
Average number of species	12	22	12	12	11	15	6	20	18	17	14	21
Mylia anomala	.	.	23**	.	.	.	.	.	.	.	.	.
Vaccinium vitis-idaea	6	13	53**	14	.	.	19	.	.	.	.	.
Sphagnum flexuosum	.	.	23**	.	.	.	.	.	.	.	.	.
Sphenolobus minutus	.	.	17*	.	.	.	.	.	.	.	.	.
Sphagnum fallax	.	13	33*	11	.	.	13	.	.	.	.	.
Sphagnum capillifolium	24	27	57*	44	19	.	38	.	.	.	.	.
Oxycoccus palustris	.	.	20*	.	.	.	13	.	.	.	.	.
1.1.1.4. *Sphagno capillifolii-Caricetum canescentis*												
Sphagnum russowii	26	.	.	56**	.	22	.	.	.	.	.	.
Avenella flexuosa	29	27	10	47*	.	13	13	.	.	.	.	.
Polytrichum commune	35	40	30	58*	25	22	12	.	.	.	.	.
2. *Scheuchzerio palustris-Caricetea nigrae*												
2.1. *Caricetalia nigrae*												
2.1.1. *Caricion canescenti-nigrae*												
2.1.1.1. *Drepanocladetum exannulati*												
Warnstorfia exannulata	.	40	.	.	100**	48	19	11	.	24	.	.
2.1.1.2. *Calliergo sarmentosi-Eriophoretum angustifolii*												
Calliergon sarmentosum	.	27	.	.	20	88**	.	25	.	10	.	.
Carex panicea	.	.	.	.	.	35**	.	.	.	.	.	.
Eriophorum angustifolium	26	.	.	19	48	70**	.	.	.	.	.	.
Juncus filiformis	21	.	17	31	37	78**	.	11	9	.	.	.
Viola palustris	.	.	.	.	.	26**	.	.	.	.	.	.
Carex nigra	56	13	.	44	60	83*	19	.	13	12	.	19
Potentilla erecta	.	.	.	.	.	17*	.	.	.	.	.	.
Sphagnum teres	.	.	.	.	.	13*	.	.	.	.	.	.
Sphagnum subsecundum	.	.	.	.	.	13*	.	.	.	.	.	.
Carex echinata	15	.	10	6	17	39*	13	.	.	.	.	.
2.2. *Scheuchzerietalia palustris*												
2.2.1. *Sphagnion cuspidati*												
Sphagnum cuspidatum	.	.	.	.	.	.	63**	.	.	.	.	.
Carex limosa	.	.	.	.	.	.	56**	.	.	.	.	.
Carex rostrata	9	.	.	8	8	.	69**	.	.	.	.	.
Warnstorfia fluitans	.	.	27	.	.	.	63**	.	.	.	.	.
Scheuchzeria palustris	.	.	.	.	.	.	13*	.	.	.	.	.
3. *Montio-Cardaminetea*												
3.1. *Montio-Cardaminetalia*												
3.1.1. *Dichodontio palustris-Swertion perennis*												
3.1.1.1. *Calthetum laetae*												
Alchemilla sp. div.	.	.	.	.	10	9	.	78*	61	41	32	51
Rhizomnium punctatum	.	.	.	.	.	.	.	33*	9	.	12	8
Doronicum austriacum	.	.	.	.	.	.	.	14*	.	.	.	.
Marchantia polymorpha	.	.	.	.	.	.	.	22*	.	8	.	.
3.1.1.2. *Caltho-Dicranelletum squarrosae*												
Dicranella palustris	.	.	.	.	.	9	.	17	96**	31	15	21
Scapania undulata	.	.	.	.	23	9	.	28	70**	35	21	17
Senecio subalpinus	.	.	.	.	10	13	.	33	57*	22	11	21
Aconitum firmum	.	.	.	.	.	.	.	61	70*	45	57	43
3.1.1.3. *Crepido paludosae-Philonotidetum seriatae*												
Pohlia wahlenbergii	.	.	.	.	.	.	.	14	.	43*	32	.
Epilobium nutans	.	.	.	.	23	.	.	.	17	37*	7	.

Group number	1	2	3	4	5	6	7	8	9	10	11	12
Number of vegetation plots	34	15	30	36	52	23	16	36	23	51	81	53
Average number of species	12	22	12	12	11	15	6	20	18	17	14	21
Dichodon cerastoides	.	13	.	.	23	.	.	8	9	37*	6	.
3.1.1.4. *Cardaminetum opicii*												
Stellaria nemorum agg.	.	.	.	.	.	.	.	25	9	43	79**	11
Cardamine amara subsp. *opicii*	.	.	.	.	10	.	.	47	26	61	95**	21
Epilobium alsinifolium	.	.	.	.	.	.	.	28	48	43	84**	64
Brachythecium rivulare	.	.	.	.	10	.	.	44	.	27	59**	11
Philonotis fontana	.	.	.	.	.	9	.	.	.	12	33*	.
Palustriella decipiens	.	.	.	.	.	9	.	33	17	29	53*	23
3.1.2. *Cratoneurion commutati*												
3.1.2.1. *Cardamino opicii-Cratoneuretum falcati*												
Palustriella commutata	.	.	.	.	.	.	.	11	13	8	25	81**
Saxifraga aizoides	.	.	.	.	.	.	.	.	.	.	.	42**
Arabis soyeri	.	.	.	.	.	.	.	.	.	.	.	26**
Cratoneuron filicinum	.	.	.	.	.	.	.	11	.	.	.	34**
Cortusa matthioli	.	.	.	.	.	.	.	.	.	.	.	17*
Pinguicula alpina	.	.	.	.	.	.	.	.	.	.	.	19*
Sesleria albicans	.	.	.	.	.	.	.	.	.	.	.	15*
Philonotis calcarea	.	.	.	.	.	.	.	.	.	.	.	17*
Bellidiastrum michelii	.	.	.	.	.	.	.	.	.	.	.	17*
Allium schoenoprasum	.	.	.	.	.	.	.	.	.	.	.	11*
Festuca carpathica	.	.	.	.	.	.	.	.	.	.	.	11*
Carex flacca	.	.	.	.	.	.	.	.	.	.	.	15*
Swertia perennis	.	.	.	.	21	22	.	33	22	.	.	49*
Parnassia palustris	.	.	.	.	.	.	.	.	.	.	.	13*
Species reaching frequency 50% in at least one column												
Polytrichum strictum	21	73**	60*	28	10		19	.	.	.	.	.
Sphagnum girgensohnii	24	60**	7	50*	10	.	.	.	.	.	.	.
Eriophorum vaginatum	85	100*	100*	81	40	35	56	.	.	.	.	.
Caltha palustris subsp. *laeta*	.	.	.	.	69	48	.	100*	96*	61	48	68
Silene pusilla	.	.	.	.	.	.	.	11	74**	37	26	66*
Viola biflora	.	.	.	.	.	17	.	64	91**	59	32	83*
Philonotis seriata	.	.	.	.	54	22	.	56	83*	88*	36	40
Bryum pseudotriquetrum	.	.	.	.	12	26	.	69	48	55	52	70
Poa alpina	.	13	.	.	13	.	.	36	22	53	38	40
Luzula alpinopilosa	.	27	.	14	27	.	.	42	22	50	19	15
Deschampsia cespitosa	12	53	.	25	50	61	.	92	96	71	44	74
Nardus stricta	74	27	.	67	37	74	.	36	48	22	.	17
Ligusticum mutellina	41	80	.	47	40	39	.	61	61	45	27	32

Campanula alpina, *Oreochloa disticha*, *Festuca picturata*, *Carex atrata*, *Carex sempervirens*), clearly distinguishing it from other subalpine types of bog. It is the most species-rich bog community above the timberline (mean number of species 22).

This community develops on flat bottoms of glacial valleys. The water level is high throughout the year and in winter the bogs are covered by a deep layer of snow. The peat layer is usually 0.2–1.2 m thick (Krajina 1933).

This community was recorded at altitudes of 1550–2100 m in the Slovakian and Polish part of the Vysoké Tatry Mts. The water pH was 4.0–5.8 and conductivity 16–33 μS·cm^{-1}.

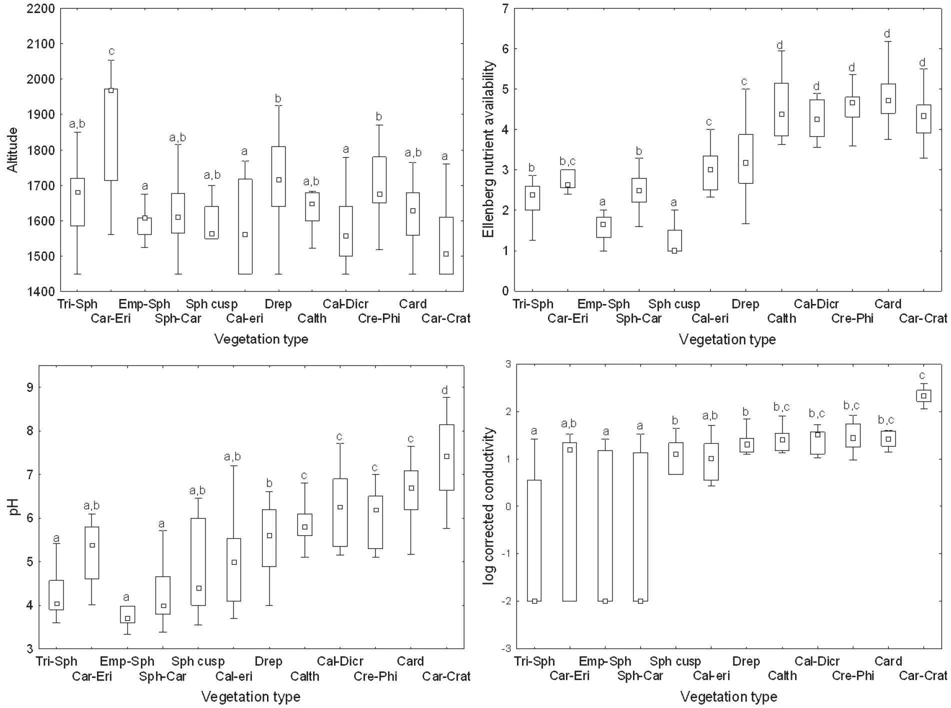


Fig. 2. – Box and whisker plots of environmental variables (water pH, corrected water conductivity, altitude) and Ellenberg nutrient availability in particular vegetation types. Boxes and whiskers show medians and 50% and 95% percentiles. Significant differences among regions (Tukey's post-hoc test) are marked by indices (a, b, c, d). Abbreviations of syntaxa names: Tri-Sph (*Trichophoro cespitosi-Sphagnetum compacti*), Car-Eri (*Carici lachenalii-Eriophoretum vaginati*), Emp-Sph (*Empetro nigri-sphagnetum fusci*), Sph-Car (*Sphagno capillifolii-Caricetum canescentis*), Sph cusp (*Sphagnion cuspidati*), Cal-Eri (*Calliergo sarmentosi-Eriophoretum angustifolii*), Drep (*Drepanocladetum exannulati*), Calth (*Calthetum laetae*), Cal-Dicr (*Caltho-Dicranelletum squarrosae*), Cre-Phi (*Crepido paludosae-Philonotidetum seriatae*), Card (*Cardaminetum opicii*), Car-Crat (*Cardamino opicii-Cratoneuretum falcati*).

3. *Empetro nigri-Sphagnetum fusci* Osvald 1923

Nomen conservandum propositum
Orig. (Osvald 1923): *Empetrum nigrum-Sphagnum fuscum*-Ass.
Syn.: *Empetro hermaphroditi-Sphagnetum fusci* Du Rietz 1926, *Sphagnetum fusci* Luquet 1926, *Rubo chamaemori-Sphagnetum fusci* Persson 1961, *Sphagno robusti-Empetretum hermaphroditi* Hadač et Váňa 1967 p.p.

This bog community is dominated by *Sphagnum fuscum* and by small shrubs (*Empetrum nigrum* agg., *Oxycoccus microcarpus*, *Oxycoccus palustris*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*) and *Eriophorum vaginatum* in the less productive herb layer. Other species of the genera *Sphagnum* (*Sphagnum magellanicum, S. rubellum, S. capillifolium, S. flexuosum, S. fallax*) and *Polytrichum* (*Polytrichum commune, P. strictum*) frequently occur.

This community develops in open bogs on flat relief. The peat layer is 0.75–0.9 m thick (Hadač et al. 1969b) and remains wet throughout the year.

This community was recorded at altitudes of 1400–1700 m in the Slovakian part of the Vysoké Tatry Mts. The water pH was 3.3–5.5 and conductivity 2–58 µS·cm^{-1}.

4. *Sphagno capillifolii-Caricetum canescentis* Hadač 1969

Nomen mutatum propositium
Orig. (Hadač et al 1969): *Sphagno nemorei-Caricetum canescentis*, ass. nova.

This subalpine small-bog community is dominated by *Sphagnum capilifolium*, *S. rusowii* and *S. girgensohnii* with the occurrence of fen species, e.g. *Juncus filiformis*, *Carex canescens* and *C. nigra* and usually a high cover of *Eriophorum vaginatum*. Some non-bog species consistently occur in the herb layer e.g. *Avenella flexuosa*, *Nardus stricta* and *Ligusticum mutellina*. In the bryophyte layer *Polytrichum commune* can make up a high percentage of the cover.

This community develops in the surroundings of glacial lakes in cirques and occurs only rarely on gentle slopes. It is a transitional type of vegetation between minerotrophic mires and ombotrophic bogs, which is influenced by ground water. The water level can reach the surface, but it never inundates the community. In the dry period the water level is 8–15 cm below ground level. The peat layer is 0.2–0.9 m thick (Hadač et al. 1969b).

This vegetation was recorded in the Vysoké Tatry Mts (both in Slovak and Polish part), Západné Tatry Mts and Nízke Tatry Mts at altitudes of 1500–1750 m. The water pH was 3.4–5.5 and conductivity 3–45 µS·cm^{-1}.

5. *Drepanocladetum exannulati* Krajina 1933

Orig. (Krajina 1933): *Drepanocladetum exannulati (brachydietyi)*
Syn.: *Caricetum fuscae subalpinum* Koch 1928, *Warnstorfia exannulata*- Gemeinschaft Dierßen 1993

This poor-fen vegetation is characterized by the strong dominance of *Warnstorfia exannulata* and the sparse occurrence of vascular plants (*Eriophorum angustifolium*, *E. vaginatum*, *Carex nigra*, *C. canescens*, *C. echinata*, *Juncus filiformis* and *Caltha palustris* subsp. *laeta*). The community is species-poor with a mean number of 11 species.

It usually develops at sites where cold mineral-poor groundwater flows across acidic bedrock. This low-productivity community is the initial fen successional stage that develops in the surroundings of springs and lakes. The peat layer is shallow.

This community was recorded in the Vysoké Tatry Mts (both in Slovak and Polish part), Západné Tatry Mts and Nízke Tatry Mts at altitudes of 1450–2100 m. The water pH was 4.0–6.3 and conductivity 6–42 µS·cm^{-1}.

6. *Calliergo sarmentosi-Eriophoretum angustifolii* Hadač et Váňa 1967

Orig. (Hadač & Váňa 1967): *Calliergo sarmentosi-Eriophoretum angustifolii* Nordhagen 1928
Syn.: *Eriophoretum polystachyi* Nordhagen 1928 (§ 3d, § 36), *Calliergonetum sarmentosi* Dahl 1957 (§ 29b), *Caricetum rostratae* Osvald 1923 *calliergonetosum sarmentosi* Steiner 1992, *Drepanoclado intermedii-Trichophoretum caespitosi* auct. non Nordhagen 1928.

This poor-fen vegetation is dominated by *Calliergon sarmentosum*. *Eriophorum angustifolium* and *Carex nigra* accompanied by *Carex panicea*, *C. echinata*, *C. canescens*, *Juncus filiformis*, *Eriophorum vaginatum*, *Viola palustris* and *Caltha palustris*. In the bryophyte layer *Warnstorfia exannulata* or *Philonotis serriata* are also common and *Sphagnum teres* and *S. subsecundum* sporadically make up a small percentage of the cover. The community is species-poor (mean number of species 15).

It develops in habitats influenced by slowly flowing, cold, mineral-poor water and is often found in the surroundings of bogs. The productivity of this community is low and the layer of fen peat shallow.

This community was recorded at altitudes of 1400–1800 m in the Vysoké Tatry Mts (both the Slovak and Polish part), Západné Tatry Mts, Nízke Tatry Mts and Malá Fatra Mts. The water pH was 3.7–6.7 and conductivity 6–51 µS·cm^{-1}.

7. *Carici rostratae-Drepanocladetum fluitantis* Hadač et Váňa 1967

Orig. (Hadač & Váňa): *Carici rostratae-Drepanocladetum fluitantis* assoc. nova (*Drepanocladus fluitans* = *Warnstorfia fluitans*)
Syn.: *Carici rostratae-Sphagnetum cuspidati* Osvald 1923 (§ 3d)

The herb layer of this community is dominated by *Carex rostrata*, which is often accompanied by *Eriophorum angustifolium* and submersed bryophytes (*Sphagnum cuspidatum, Warnstorfia fluitans*). It is usually very species-poor, but those on lake shores can be more species-rich, with species characterizing poor fens present (e.g. *Carex canescens*, *C. echinata* or *Juncus filiformis*). The herb layer is variously developed with the covers ranging from 1 to 75%, but bryophytes can cover the whole surface.

This community develops in bog hollows and on the shores of glacial lakes where the depth of the peat layer is shallow and roots of sedges can therefore reach the mineral soil. Water level is high. The water pH was 3.6–6.5 and conductivity 13–44 µS·cm^{-1}. This community was found at altitudes below 1700 m a.s.l. in the Vysoké Tatry Mts (both in Slovakia and Poland).

8. *Drepanoclado fluitantis-Caricetum limosae* (Kästner et Flössner 1933) Krisai 1972

Orig. (Krisai 1972): *Drepanoclado fluitantis-Caricetum limosae* (Kästner et Flössner 1933) Krisai 1972 (*Drepanocladus fluitans* = *Warnstorfia fluitans*)
Syn.: *Caricetum limosae* Br.-Bl. 1921 p. p. (§ 36), *Carici limosae-Sphagnetum cuspidati* Osvald 1923 (§ 3d), *Scheuchzerio-Sphagnetum cuspidati* Osvald 1923 (§ 3d), *Sphagno lindbergii-Caricetum limosae* Osvald 1923 (§ 3d), *Caricetum limosae drepanocladetosum fluitantis* Kästner et Flössner 1933 (§ 36)

This community formed the same cluster as the previous one and is dominated by *Carex limosa* and submerged bryophytes (*Sphagnum cuspidatum* or *Warnstorfia fluitans*) often with *Carex rostrata* in the herb layer. It is very species-poor with a mean number of five species. The herb layer cover is low, whereas that of bryophytes is usually 100%.

This community was found in a bog complex overgrowing a glacial lake, where it occurred mainly along the lake shore. The dominant species are adapted to a high water table and a very acidic and dystrophic environment.

The water pH was 3.8–4.4 and conductivity 15–35 µS·cm^{-1}. In the subalpine belt the community was sampled at only one locality at an altitude of approximately 1550 a.s.l. (Mlynické pliesko) in the Slovakian part of the Vysoké Tatry Mts. However, it occurs in a few localities at lower altitudes.

9. *Calthetum laetae* Krajina 1933

Orig. (Krajina 1933): *Calthetum laetae*
Syn.: *Calthetum palustris* Sillinger 1933, *Aconito-Philonotidetum serriatae* Hadač 1956, *Philonotido-Calthetum laetae* (Krajina 1933) Coldea 1991

The herb layer of this productive type of vegetation associated with springs in the subalpine belt is dominated by broad-leaved *Caltha palustris* subsp. *laeta*, which is often accompanied by *Alchemilla* sp. div., *Aconitum firmum* and *Doronicum austriacum*. The bryophyte cover is usually lower than 30%. The most abundant species are *Rhizomnium punctatum*, *Brachythecium rivulare*, *Philonotis seriata* and *Bryum pseudotriquetrum*. The mean number of species in this community is 20. It is also found in less waterlogged areas with long lasting snow cover and slowly flowing water, mostly on gentle slopes.

The water pH was 5.4–7.3 and conductivity 16–80 $\mu S \cdot cm^{-1}$. This community was found at altitudes below 1955 m a.s.l. in the Malá Fatra Mts, Nízke Tatry Mts, Vysoké Tatry Mts (both in Slovakia and Poland) and Západné Tatry Mts.

10. *Caltho-Dicranelletum squarrosae* Hadač 1956

Orig. (Hadač 1956): *Caltheto-Dicranelletum squarrosae*
Syn.: *Epilobio-Cratoneuretum filicini* Hadač 1956

This productive high-mountain vegetation associated with springs is characterized by *Caltha palustris* subsp. *laeta.* This species can be less abundant than in the former community. It is often accompanied by *Silene pusilla*, *Senecio subalpinus* and *Viola biflora*. The percentage cover of bryophytes is usually high and mainly made up of *Scapania undulata* and *Dicranella palustris*. The mean number of species in this community is 18.

This community develops in springs with shallow stoney soils or in the surroundings of small streams that are permanently saturated with running water on slight to steep slopes.

The water pH was 5.4–7.7 and conductivity 13–53 $\mu S \cdot cm^{-1}$. This community was found at altitudes usually below 1650 m a.s.l. in the Malá Fatra Mts, Nízke Tatry Mts, Vysoké Tatry Mts (both in Slovakia and Poland) and Západné Tatry Mts.

11. *Crepido paludosae-Philonotidetum seriatae* Hadač et Váňa 1972

Orig. (Hadač & Váňa 1972): *Crepidi-Philonotidetum seriatae* Hč et Váňa, assoc. nova (*Crepis paludosa*)
Syn.: *Mniobryetum albicantis* Šmarda 1950 (§ 29b), *Epilobio alsinifolii-Philonotidetum seriatae* Jeník et al. 1980, *Aconito-Philonotidetum seriatae* Hadač 1956

This vegetation occurs in mineral-poor and acidic springs and is dominated by the bryophytes *Philonotis seriata* or *Pohlia wahlenbergii*. Other common bryophytes are *Palustriella decipiens*, *Dicranella palustris*, *Bryum pseudotriquetrum* and *Scapania undulata*. The percentage cover of the herb layer is variable, with *Deschampsia cespitosa, Caltha palustris* subsp. *laeta* and *Viola biflora* the most frequently occurring species and *Dichodon cerastoides* and *Epilobium nutans* the diagnostic species. The mean number of species in this community is 17.

This subalpine spring community develops on granite bedrock with steady flowing water, on gentle to steep slopes. The water is cold, mineral-poor and acidic to neutral.

The water pH was 5.4–7.0 and conductivity 11–53 $\mu S \cdot cm^{-1}$. This community was usually found at altitudes below 1850 m a.s.l. in the Nízke Tatry Mts, Vysoké Tatry Mts (both in Slovakia and Poland) and Západné Tatry Mts.

12. *Cardaminetum opicii* Szafer et al. 1923

Orig. (Szafer et al. 1923): *Cardaminetum Opicii*
Syn.: *Cardaminetum opicii* Krajina 1933, *Cardaminetum opicii* Šmarda 1950, *Brachythecio rivularis-Cardaminetum opicii* (Krajina 1933) Hadač 1983

This highly productive spring vegetation is dominated by *Cardamine amara* subsp. *opicii*. It has a tall growing herb layer consisting of *Cardamine amara* subsp. *opicii*, *Aconitum firmum*, and *Caltha palustris* subsp. *laeta*. Below their canopy other spring specialists occur, such as the vascular plants *Stellaria nemorum*, *Chrysosplenium alternifolium* and *Epilobium alsinifolium* and mosses *Palustriella decipiens*, *Brachythecium rivulare*, *Philonotis fontana* and *Bryum pseudotriquetrum*. The community can be either species-poor or species-rich (4–33 species). The species richness is low if *Cardamine amara* dominates strongly.

This type of vegetation can usually be found in springs on gentle slopes or around small streams of cold water, which are protected from the wind. The water pH was 5.9–7.2 and conductivity 16–53 μS·cm^{-1}. This community was found at altitudes below 1750 m a.s.l. in the Nízke Tatry Mts, Vysoké Tatry Mts (both in Slovakia and Poland) and Západné Tatry Mts.

13. *Cardamino opicii-Cratoneuretum falcati* Szafer et Sokolowski 1927

Orig. *Cratoneuron falcatum-Cardamine opizii* Assoziation
Syn.: *Cratoneuretum falcati* Gams 1927, *Cratoneuro-Saxifragetum aizoidis* Hadač 1983, *Palustriella commutata-Arabis jacquini* Koch 1928, *Arabido-Cratoneuretum* Pawlowski 1956, *Swertio-Caricetum claviformis* (Hadač et al. 1969) Hadač 1983

This productive spring community occurs on limestone bedrock and is dominated by bryophytes of the genus *Palustriella* (*Palustriella commutata* subsp. *falcata*, *P. decipiens*), which tolerate alkaline conditions. The dominant *Palustriella* species are usually accompanied by *Philonotis calcarea* and *Aneura pinguis*. More diagnostic species can be found in the herb layer (e.g., *Saxifraga aizoides*, *Arabis soyeri*, *Pinguicula alpina*, *Carex flacca*, *Corthusa matthioli*, *Bellidiastrum michelii*).

This community can develop on very steep slopes and prefers water with a constantly high pH. The water pH was 6.0–8.8 and conductivity 45–395 μS·cm^{-1}. This community was recorded at altitudes below 1750 m a.s.l. in the Malá Fatra Mts, Nízke Tatry Mts, Západné Tatry Mts and Belianske Tatry Mts, always on limestone.

Ecological determinants of floristic composition

The most important gradients revealed by the DCA analysis of the entire data set revealed the major directions of floristic variation along two principal axes (eigenvalues 0.778 and 0.289). First, the strongly dominant axis stretches from bogs through fens to springs and reflects differences in water pH and Ellenberg's nutrients. The second axis correlates with altitude and corrected conductivity (Fig. 3). When springs and mires are analysed separately, different environmental determinants of vegetation variation emerge. The main ecological gradients in the subsets differ from each other and from that obtained by the analysis of the entire data set. In the spring subset corrected water conductivity, water pH and altitude combined with slope inclination are the most important (Table 2). In the fen subset and bog subset altitude is more important than water pH and corrected conductivity. In all cases geomorphology (shape of the valley) is also important. The fens and bogs are more tightly influenced by geomorphological conditions than springs.

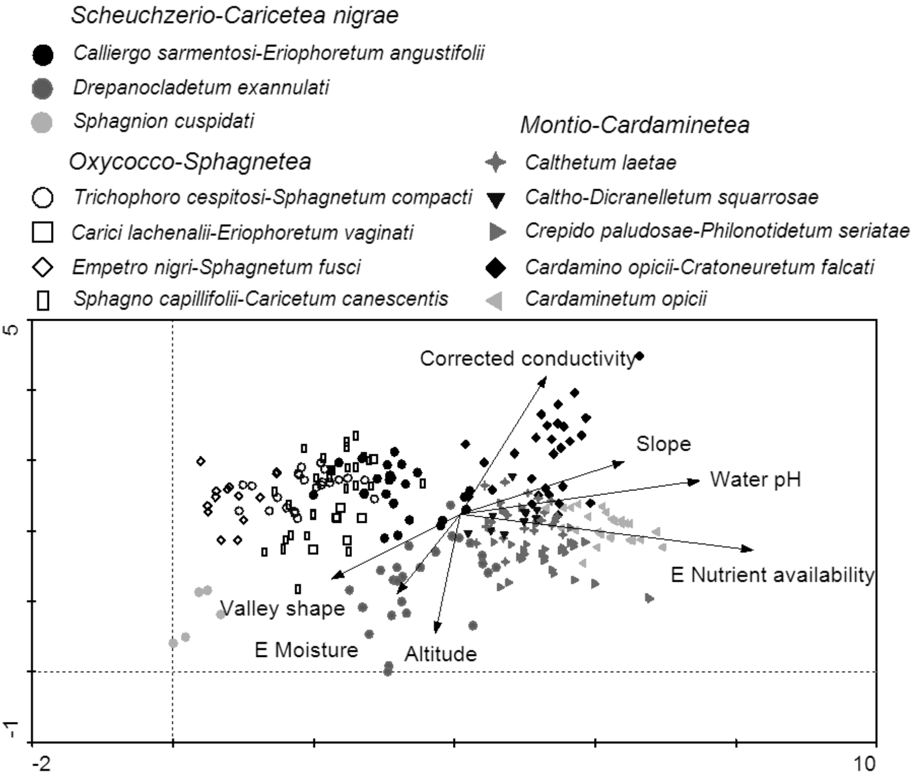


Fig. 3. – Detrended correspondence analysis (DCA) ordination diagram of the entire data set with Ellenberg indicator values plotted a posteriori onto the scatter. Particular clusters are indicated by different symbols. First two axes are presented, eigenvalues: 1st axis 0.78, 2nd axis 0.29. Valley shape is an ordinal variable (1: narrow, V-shaped; 2: wider V-shaped; 3: wide U-shaped; 4: very wide, U-shaped with glacial lakes), E: Mean of Ellenberg indicator values per plot.

Species richness (α-diversity)

The corrected species richness differed significantly among particular vegetation types (Table 3). The bog association enriched by the species from neighbouring vegetation (*Carici lachenalii-Eriophoretum vaginati*), subalpine productive spring vegetation (*Calthetum laetae*) and spring vegetation on alkaline bedrock (*Cardamino opicii-Cratoneuretum falcati*) are the most species-rich vegetation types (mean number of species 22, 21 and 20, respectively). In contrast, the bog hollow vegetation (*Sphagnion cuspidati*), which occupies extremely acidic and dystrophic habitats, is extremely species-poor (mean number of species is 6). The environmental factors that were correlated with the corrected α-diversity of vascular plants differed from the environmental factors influencing bryophytes. Moreover, different factors were important for different classes of vegetation (spring, bog, fen vegetation) (Table 4). In the spring subset only corrected conductivity (approximating total mineral richness) and water pH explained a significant amount of the variation in vascular-plant corrected α-diversity. For bryophytes the most important factor was the slope inclination and the corrected conductivity, while pH was not significant. In the fen subset the corrected

Table 2. – The results of the stepwise selection of the environmental variables using forward selection procedure in CCA analysis. Valley shape is an ordinal variable (1: narrow, V-shaped, 2: wider V-shaped, 3: wide U-shaped, 4: very wide, U-shaped with glacial lakes).

Step	Environmental variables	F-ratio	P-value	%
Entire data set				
1	Water pH	14.19	0.001	5.7
2	Corrected conductivity	4.36	0.001	1.6
3	Altitude	3.53	0.001	1.3
4	Slope inclination	2.80	0.001	1
5	Valley shape	2.46	0.001	
Spring subset (*Montio-Cardaminetea*)				
1	Corrected conductivity	4.86	0.001	4.1
2	Water pH	2.88	0.002	2.7
3	Altitude	2.80	0.002	2.1
4	Slope inclination	2.31	0.002	1.4
5	Valley shape	2.00	0.002	
Fen subset (*Scheuchzerio-Caricetea nigrae*)				
1	Altitude	2.75	0.001	6
2	Valley shape	2.36	0.002	4.2
3	pH	1.85	0.032	2.4
4	Corrected conductivity	1.59	0.038	2.1
Bog subset (*Oxycocco-Sphagnetea*)				
1	Altitude	3.91	0.001	5.4
2	Valley shape	1.87	0.009	2.7
3	pH	1.64	0.018	1.9

Table 3. – Descriptive statistics of the total number of inventoried species in particular vegetation types. Plots – the total number of vegetation plots, Mean – the mean number of species per plot. Tri-Sph (*Trichophoro cespitosi-Sphagnetum compacti*), Car-Eri (*Carici lachenalii-Eriophoretum vaginati*), Emp-Sph (*Empetro nigri-sphagnetum fusci*), Sph-Car (*Sphagno capillifolii-Caricetum canescentis*), Sph cusp (*Sphagnion cuspidati*), Cal-Eri (*Calliergo sarmentosi-Eriophoretum angustifolii*), Drep (*Drepanocladetum exannulati*), Calth (*Calthetum laetae*), Cal-Dicr (*Caltho-Dicranelletum squarrosae*), Cre-Phi (*Crepido paludosae-Philonotidetum seriatae*), Card (*Cardaminetum opicii*), Car-Crat (*Cardamino opicii-Cratoneuretum falcati*). Significant differences in residual species richness (controlled for log-transformed plot size) per plot among vegetation types (Tukey's post-hoc test) are marked by indices (a, b).

Vegetation	Plots	All species				Vascular plants				Bryophytes			
type		Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Bogs (*Oxycocco-Sphagnetea*)													
Tri-Sph	34	12.2^{a}	3	21	4.17	8.6^{a}	2	16	3.7^{a}	3.5	1	8	1.5
Car-Eri	15	21.8^{a}	10	39	8.3	14.2^{ab}	5	27	6.2^{a}	7.6	2	16	4.1
Emp-Sph	30	11.5^{a}	6	18	2.9	5.6^{a}	2	11	2.2^{a}	5.9	3	9	1.6
Sph-Car	36	12.2^{a}	6	23	4.7	7.9^{a}	1	17	3.4^{a}	4.2	1	10	2.1
Fens (*Scheuchzerio-Caricetea nigrae*)													
Sph cusp	16	6.4^{a}	1	17	4.4	3.2^{a}	1	10	2.8^{a}	3.1	0	7	1.6
Drep	52	11.2^{a}	3	22	5.7	7.1^{a}	1	16	3.9^{a}	4.1	1	10	2.4
Cal-Eri	23	15^{ab}	8	30	5.6	9.8^{a}	5	18	3.1^{a}	5.2	1	13	3.5
Springs (*Montio-Cardaminetea*)													
Calth	36	20.4^{b}	9	47	8.6	13.5^{b}	6	35	6.3^{b}	6.9	2	15	3.4
Cal-Dicr	23	17.8^{ab}	7	40	7.1	$12.1^{a,b}$	5	22	4.3^{ab}	5.8	2	18	3.5
Cre-Phi	51	17^{ab}	7	29	5.7	11^{a}	4	22	4.2^{ab}	6.0	2	15	3.0
Car-Crat	53	20.7^{b}	3	41	9.2	15.5^{b}	2	31	7.4^{b}	5.2	1	21	4.4
Card	81	14.4^{a}	4	33	6.2	8.7^{a}	1	24	4.6^{b}	5.6	1	15	3.0

Table 4. – Results of general regression models (linear or quadratic) testing separately the relationships between corrected plant α-diversity and environmental factors for bryophytes and vascular plants. Percentage variance accounted for by the whole regression model is presented as the adjusted R^2 statistics. *P < 0.05; **P < 0.01; ***P < 0.001; n.s., non-significant.

		F-ratio			
Vegetation type	Environmental factor	linear	quadratic	R^2_{Adj}	Shape
Spring subset (*Montio-Cardaminetea*)					
Vascular plants	Water pH	7.3**	8.2**	7.1%	J-shaped
	Corrected conductivity	9.2**	7.2**	10.0%	unimodal
	Altitude	n.s.	n.s.	n.s.	
	Slope inclination	n.s.	n.s.	n.s.	
Bryophytes	Water pH	n.s.	n.s.		
	Corrected conductivity	6.5*	7.7**	10.9%	unimodal
	Altitude	4.4*	n.s.	2.7%	increasing
	Slope inclination	18.9*	n.s.	13.4%	increasing
Fen subset (*Scheuchzerio-Caricetea nigrae*)					
Vascular plants	Water pH	21.0***	n.s.	28.1%	increasing
	Corrected conductivity	6.9*	n.s.	10.4%	increasing
	Altitude	n.s.	n.s.	n.s.	
	Slope inclination	n.s.	n.s.		
Bryophytes	Water pH	12.7***	n.s.	18.7%	increasing
	Corrected conductivity	10.3**	n.s.	15.4%	increasing
	Altitude	n.s.	n.s.	n.s.	
	Slope inclination	n.s.	n.s.	n.s.	
Bog subset (*Oxycocco-Sphagnetea*)					
Vascular plants	Water pH	8.5**	n.s.	9.6%	increasing
	Corrected conductivity	n.s.	n.s.		
	Altitude	8.3**	n.s.	9.3%	increasing
	Slope inclination	n.s.	n.s.		
Bryophytes	Water pH	n.s.	n.s.		
	Corrected conductivity	n.s.	n.s.		
	Altitude	n.s.	n.s.		
	Slope inclination	n.s.	n.s.		

α-diversity of both vascular plants and bryophytes was connected with water pH and corrected conductivity. The α-diversity of vascular plants in the bog vegetation was influenced by water pH and altitude. None of the factors measured significantly affected species richness of bryophytes in bogs.

Discussion

Syntaxonomy and classification within higher syntaxa

The wetland vegetation in the (sub)alpine belt of the West Carpathians has not been previously systematically investigated or synthesized. During this research 13 associations were recorded and classified within five alliances and three classes. Three of them are not included in the latest national vegetation survey (Valachovič 2001). In one case it is suggested that two associations be merged into one, because they are not clearly differentiated in terms of floristic composition, and in a few cases it is suggested that the association names be revised according to the rules of phytosociological nomenclature (Weber et al. 2000).

The associations not included in the latest national vegetation survey (Valachovič 2001) are *Sphagno capillifolii-Caricetum canescentis* Hadač 1969, *Calliergo sarmentosi-Eriophoretum angustifolii* Hadač et Váňa 1967 and *Crepido paludosae-Philonotidetum seriatae* Hadač et Váňa 1972. Some of the vegetation of the latter association is also included in the association *Mniobryetum albicantis* Šmarda 1950. The *Sphagno capillifolii-Caricetum canescentis* association was previously described on the basis of three vegetation plots in the same study area (Hadač et al. 1969b), but was not accepted in later vegetation surveys. However, new material collected during this study led to its clear differentiation as a bog community with some fen species. Hadač includes this association in the *Caricion canescenti-nigrae* alliance, but in the analyses presented it has a greater affinity to the *Oxycocco microcarpi-Empetrion hermaphroditi* alliance. This association differs from the *Sphagnum*-dominated vegetation that is found on gentle or steep slopes independent of ground water in the high mountains of the West Carpathians, which is included in the association *Sphagno capillifolii-Empetretum nigri* Bělohlávková in Šibík et al. 2006 (Šibík et al. 2006, Sekulová & Hájek 2009). The difference lies in the influence of mineral water and therefore the presence of fen species, while in the case of the *Sphagno capillifolii-Empetretum nigri* (corresponding to "Kondenswassermoore" of Steiner 1992) no fen species are present. An ecologically and successionally analogical community to *Sphagno capillifolii-Caricetum canescentis* occurs in the Bulgarian mountains (Hájek et al. 2005, Hájková et al. 2006) and is assigned to the association *Bruckenthalio-Sphagnetum capillifolii*. The poor fen community *Calliergo sarmentosi-Eriophoretum angustifolii* occurs in the Krkonoše Mountains in the Czech Republic (Hadač & Váňa 1967). It is floristically well differentiated from the other poor fen association *Drepanocladetum exannulati* by a high constancy of *Calliergon sarmentosum*, which is usually abundant. While *Drepanocladetum exannulati* is moss-dominated vegetation with a very sparse herb layer, many fen species, such as *Juncus filliformis*, *Carex nigra*, *Carex panicea* and *Eriophorum angustifolium,* are common in *Calliergo sarmentosi-Eriophoretum angustifolii*. Hadač & Váňa (1967) state that this vegetation type was first recognized and validly described by Nordhagen (1928; orig. "*Calliergon sarmentosum*-reiche *Eriophorum polystachyum*-Ass."). Both the poor fen associations *Calliergo sarmentosi-Eriophoretum angustifolii* and *Drepanocladetum exannulati* are included here in the order *Caricion canescenti-nigrae*. Due to the lack of diagnostic species and its poor floristic differentiation from the alliance *Caricion canescenti-nigrae*, the alliance *Drepanocladion exannulati* was not recognized in this study. The *Drepanocladion exannulati* alliance in the West Carpathians (Krajina 1933, Hájek & Háberová 2001) was established to highlight the difference in ecology and vegetation of submontane *Caricion nigrae* meadows and subalpine spring fens. The alliance was accepted by Rybníček et al. (1984), Valachovič (2001) and Chytrý & Tichý (2003) but not by most authors (Steiner 1993, Dierßen 1996, Rodwell et al. 2002, Matuszkiewicz 2007).

In this analysis the two associations of calcareous springs distinguished in the latest survey (*Cratoneuretum falcati* Gams 1927 and *Cratoneuro-Saxifragetum aizoidis* Hadač 1956) were not separated. Because the calcareous springs in the West Carpathians seem to differ from those in the Alps (Kliment et al. 2008), the name *Cardamino opicii-Cratoneuretum falcati* Szafer et Sokolowski 1927 was used instead of *Cratoneuretum* *falcati* Gams 1927. To clarify the syntaxonomy of calcareous *Palustriella*-dominated springs, further investigations are needed throughout Europe. Further we do not use the alliance *Cratoneuro filicini-Calthion laetae* Hadač 1983 that should include West-Carpathian subalpine springs, even if this alliance is accepted by some authors (e.g. Valachovič 2001, Hrivnák et al. 2004, Kliment et al. 2008), as this alliance displays very similar ecology and floristic composition to that of the alliance *Dichodontio palustris-Swertion perennis* Hadač 1983. Matuszkiewicz (2007) includes the same vegetation in the alliance *Cardamino-Montion* Br.-Bl. 1925. Zechmeister & Mucina (1994) in their review of high-rank spring syntaxa regard both of the latter names as suballiances of different alliances (montane alliance *Caricion remotae* Kästner 1941 and alpine alliance *Cardamino-Montion* Br.-Bl. 1926 em. Zechmeister 1993, respectively).

The syntaxonomical system presented in this study can be also used for (sub)alpine wetlands in the neighbouring Suddeten mountains (Czech Republic, Poland). Nevertheless, two associations recorded in the Suddeten mountains are not found in the West Carpathians (*Swertietum perennis* Zlatník 1928 and *Bartsio alpinae-Caricetum nigrae* Bartsch et Bartsch 1940).

Ecological determinants of vegetation diversity and species richness

In the widest and most general context, the vegetation of (sub)alpine springs can be easily differentiated on the basis of water pH and conductivity. This is consistent with most studies of European springs and mires (Gerdol 1995, Gerdol & Bragazza 2001, Hájek 2002, Hájková et al. 2008). Water pH and conductivity are the most important determinants of floristic variation even when only the vegetation of springs (*Montio-Cardaminetea*) is analysed (see also Beierkuhnlein & Gräsle 1998, Spitale et al. 2009, Strohbach et al. 2009). Spring water chemistry depends primarily upon lithology, altitude and acidification (Cantonati et al. 2006, Strohbach et al. 2009). The results presented show that slope inclination is the second most important factor associated with spring species composition and richness. Steeper slopes have a greater heterogeneity of microhabitats (e.g., more stones on the surface of the soil), faster water flow and a higher incidence of disturbance and organic sediment runoff.

Ecological differentiation of (sub)alpine wetland vegetation is governed not only by water chemistry, but also by altitude and valley shape, factors connected with mesoclimate and relictualism, respectively. Analogous to alpine tundra (Batllori et al. 2009, Wilson & Nilsson 2009), there are wetland vegetation types found only at higher altitudes, i.e. cooler, belts in the West Carpathians. The highest median altitude is that recorded for the initial-bog community of the *Carici lachenalii-Eriophoretum vaginati* association, which has a specific species combination that so far has not been found in any other mountain range. In this study, the role of altitude and geomorphology was more important for fen and bog than for spring vegetation. Although, the influence of topography on the vegetation of alpine tundra is widely accepted (Jeník 1961, Šrůtek & Doležal 2003) its influence on the vegetation diversity of wetlands is not always acknowledged. The wide subalpine valleys created by glaciers are separated from each other by steep mountain peaks, which are barriers to migration and often harbour glacial relicts (Fudali & Kučera 2003). Within fens and bogs, altitude was even more important for the floristic composition than water pH or conductivity, which contrasts with the results of studies conducted below the timberline (e.g. Hájek 2002, Bragazza et al. 2005, Marini et al. 2008). One possible reason for this is that the limestone bedrock in the (sub)alpine zone of the West Carpathians supports only spring vegetation. By analogy, Hájková et al. (2006) found that in the crystalline alpine zone of the Balkans, fen vegetation is not diversified according to the gradient of mineral richness, but according to altitude and successional stage. The different determinants of species composition of the vegetation of springs, fens and bogs confirms the usefulness of partitioning vegetation data sets into classes, as previously suggested by Wamelink et al. (2002) and Vonlanthen et al. (2006).

In this study, the major determinants of species richness were not always mirrored by the determinants of variation in species composition and in some cases were quite different. Unlike species composition, pH was the most important factor for vascular plant species richness in all the vegetation classes studied and for bryophyte richness in fens. This supports the generally accepted assumption that the floras of temperate climatic zones contain higher numbers of calcicole than calcifuge species (Hegi et al. 1977, Pärtel 2002).

Species richness patterns along various gradients often differ for different taxonomic and functional groups (Pausas & Austin 2001), such as bryophytes and vascular plants in alpine habitats (Bruun et al. 2006, Grau et al. 2007, Spitale et al. 2009). This study demonstrates the different behaviour of vascular plants and bryophytes with respect to environmental factors in different vegetation types. The most apparent differences were found for spring vegetation. Only one factor (corrected conductivity) influenced both bryophyte and vascular plant α-diversity. The vascular plant α-diversity was further influenced by pH and bryophyte α-diversity by altitude and slope inclination. The significant effect of slope inclination on bryophyte richness confirms the importance of microhabitat heterogeneity, which favours a specialized bryoflora (Vitt & Belland 1997, Bergamini et al. 2001, Vanderpoorten & Engels 2003).

Different relationships between the species richness of bryophytes and water conductivity were recorded in the different vegetation classes. For spring vegetation the relationship is unimodal, while in fens the number of bryophytes increased with increase in alkalinity and there is no trend in bogs. The relationship between the gradients in mineral richness and species richness of bryophytes is reported to be unimodal (Vitt et al. 1995, Hájková & Hájek 2003), but for this study area the gradient is incomplete as fens and bogs do not occur on limestone bedrock above the timberline. The lack of a relationship between conductivity and bryophyte species richness in bogs, as also found in *Sphagnum*-rich mires below the timberline (Hájková & Hájek 2004), may be due to the crucial role of other, unmeasured factors such as peat depth or depth of the water table (Bragazza & Gerdol 1999, Bragazza et al. 2005), site age (Hájek et al. 2011) or successional stage.

Acknowledgements

We would like to thank Drahoslava Pukajová for providing unpublished data. We also thank Ondřej Hájek for supplying the distribution map and Tony Dixon for editing our English. This study was supported by projects MSM0021622416, AVZ0Z6005908, GA526/09/H025 and GA505/10/0638.

Souhrn

Článek představuje vegetační syntézu subalpínských a alpínských mokřadů (pramenišť, minerotrofních rašelinišť a vrchovišť) celých Západních Karpat (Slovensko, Polsko), založenou nejen na databázových, ale z velké části i na vlastních datech. Klademe si za cíl rozlišit hlavní typy subalpínských a alpínských mokřadů a najít hlavní faktory prostředí, které jsou zodpovědné za variabilitu v druhovém složení a v druhové bohatosti mechorostů i cévnatých rostlin. Jako nejlépe ekologicky a fytocenologicky interpretovatelná se ukázala klasifikace vysokohorských mokřadů na úrovni 12 skupin. Na jejím základě a na základě srovnání se sousedními oblastmi jsme jasně rozlišili tři asociace, které nebyly uvedeny v posledním vegetačním přehledu Slovenska a revidovali syntaxonomické postavení a nomenklaturu jednotlivých asociací, které se často vyskytují i v sousední České republice. Představujeme tak nový klasifikační koncept vysokohorské mokřadní vegetace bývalého Československa a Polska (s výjimkou asociací *Swertietum perennis* a *Bartsio alpinae-Caricetum nigrae*, které na Slovensko nezasahují). V dalším kroku jsme se detailně zaměřili na ekologické determinanty variability v druhovém složení a druhové bohatosti. Zatímco pH určovalo rozdíly v druhovém složení mezi jednotlivými třídami a rovněž variabilita v druhovém složení pramenišť byla určována chemismem vody, variabilita v druhovém složení rašelinišť byla určována zejména nadmořskou výškou a geomorfologickými podmínkami. Druhová bohatost pramenišť třídy *Montio-Cardaminetea* byla více ovlivňována minerální bohatostí vody než pH a v případě mechorostů rovněž sklonem svahu. Druhová bohatost rašelinišť (*Scheuchzerio-Caricetea nigrae*) se zvětšovala s rostoucím pH. Naše výsledky ukazují, že ekologické gradienty, které ovlivňují variabilitu vysokohorské vegetace, se liší mezi jednotlivými biotopy.

References

Barkman J. J., Doing H. & Segal S. (1964): Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. – Acta Bot. Neerl. 13: 394–419.

Batllori E., Blanco-Moreno J. M., Ninot J. M., Gutierrez E. & Carrillo E. (2009): Vegetation patterns at the alpine treeline ecotone: the influence of tree cover on abrupt change in species composition of alpine communities. – J. Veg. Sci. 20: 814–825.

Beierkuhnlein C. & Gräsle W. (1998): The influence of light regime and water chemistry on the structure of forest spring vegetation. – In: Botosaneanu L. (ed.), Crenobiology, p. 9–22, Backhuys Publishers, Leiden.

Bergamini A., Pauli D., Peintinger M. & Schmid B. (2001): Relationships between productivity, number of shoot and number of species in bryophytes and vascular plants. – J. Ecol. 89: 920–929.

Bragazza L. & Gerdol R. (1999): Ecological gradients on some *Sphagnum* mires in the southeastern Alps (Italy). – Appl. Veg. Sci. 2: 55–60.

Bragazza L. & Gerdol R. (2002): Are nutrient availability and acidity-alkalinity gradients related in *Sphagnum*-dominated peatlands? – J. Veg. Sci.13: 473–482.

Bragazza L., Rydin H. & Gerdol R. (2005): Multiple gradients in mire vegetation: a comparison of a Swedish and an Italian bog. – Plant Ecol. 177: 223–236.

Britton A. J., Beale C. M., Towers W. & Hewison R. L. (2009): Biodiversity gains and losses: evidence for homogenisation of Scottish alpine vegetation. – Biol. Conserv. 142: 1728–1739.

Bruun H. H., Moen J., Virtanen R., Grytnes J. A., Oksanen L. & Angerbjorn A. (2006): Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. – J. Veg. Sci. 17: 37–46.

Cantonati M., Gerecke R. & Bertuzzi E. (2006): Springs of the Alps: sensitive ecosystems to environmental change: from biodiversity assessments to long-term studies. – Hydrobiologia 562: 59–96.

Chytrý M. & Tichý L. (2003): Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision. – Folia Fac. Sci. Nat. Univ. Masarykianae Brun. 108: 1–231.

Chytrý M., Tichý L. & Roleček J. (2003): Local and regional patterns of species richness in Central European vegetation types along the pH/calcium gradient. – Folia Geobot. 38: 429–442.

Cooper D. J., Wolf E. C. & Colson C. (2010): Alpine peatlands of the Andes, Cajamarca, Peru. – Arct. Antarct. Alp. Res. 42: 19–33.

Dierßen K. (1996): Vegetation Nordeuropas. – Ulmer, Stuttgart.

Ellenberg H., Weber H. E., Düll R., Wirth W., Werner W. & Paulißen D. (1992): Zeigerwerte von Pflanzen in Mitteleuropa. – Scripta Geob. 18: 1–258.

Ewald J. (2003): A critique for phytosociology. – J. Veg. Sci.14: 291–296.

Fudali E. & Kučera J. (2003): Bryogeographical elements of moss flora in glacial cirques "Śnieżne Kotły" (Karkonosze Mts) and their threat. – Acta Soc. Bot. Pol. 72: 79–85.

Gerdol R. (1995): Community and species-performance patterns along an alpine poor-rich mire gradient. – J. Veg. Sci. 6: 175–182.

Gerdol R. & Bragazza L. (2001): Syntaxonomy and community ecology of mires in the Rhaetian Alps (Italy). – Phytocoenologia 29: 271–299.

Grandin U. (2006): PC-ORD version 5: a user-friendly toolbox for ecologists. – J. Veg. Sci. 17: 843–844.

Grau O., Grytnes J. A. & Birks H. J. B. (2007): A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. – J. Biogeogr. 34: 1907–1915.

Hadač E. (1956): Rostlinná společenstva Temnosmrečinové doliny ve Vysokých Tatrách [Plant communities of Temnosmrečinová valley in Vysoké Tatry Mts]. – Biol. Práce II/1: 1–78.

Hadač E. (1983): A survey of plant communities of springs and mountain brooks in Czechoslovakia. – Folia Geob. Phytotax. 18: 339–381.

Hadač E., Březina P., Ježek V., Kubička J., Hadačová V. & Vondráček M. (1969a): Die Pflanzengesellschaften des Tales Dolina Siedmich pramenov in der Belauer Tatra. – In: Vegetácia ČSSR, B2, SAV, Bratislava.

Hadač E., Ježek V. & Březina P. (1969b): Rostlinná spoločenstvá Trojrohého plesa ve Vysokých Tatrách [Plant communities of glacial lake Trojrohé pleso in Vysoké Tatry Mts]. – Zbor. prác o TANAPe 11: 481–494.

Hadač E. & Váňa J. (1967): Plant communities of mires in the western part of the Krkonoše Mountains, Czechoslovakia. – Folia Geobot. Phytotax. 2: 213–254.

Hájek M. (2002): The class *Scheuchzerio-Caricetea fuscae* in the Western Carpathians: indirect gradient analysis, species groups and their relation to phytosociological classifcation. – Biologia 57: 461–469.

Hájek M. & Háberová I. (2001): *Scheuchzerio-Caricetea fuscae*. – In: Valachovič M. (ed.), Rastlinné spoločenstvá Slovenska 3. Vegetácia mokradí [Plant Communities of Slovakia 3. Vegetation of Wetlands], p. 185–273, Veda, Bratislava.

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., Horsák M., Hájková P. & Dítě D. (2006): Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. – Persp. Plant Ecol. Evol. Syst. 8: 97–114.

Hájek M., Horsák M., Tichý L., Hájková P., Dítě D. & Jamrichová E. (2011): Testing a relict distributional pattern of fen plant and terrestrial snail species at the Holocene scale: a null model approach. – J. Biogeogr. (in press, doi:10.1111/j.1365-2699.2010.02424).

Hájek M., Tzonev R., Hájková P., Ganeva A. & Apostolova I. (2005): Plant communities of the subalpine mires and springs in the Vitosha Mt. – Phytol. Balcan. 11: 193–205.

Hájková P. & Hájek M. (2003): Species richness and above-ground biomass of poor and calcareous spring fens in the flysch West Carpathians, and their relationship to water and soil chemistry. – Preslia 75: 271–287.

Hájková P. & Hájek M. (2004): Bryophyte and vascular plant responses to base-richness and water level gradients in Western Carpathian *Sphagnum*-rich mires. – Folia Geobot. 39: 335–351.

Hájková P., Hájek M. & Apostolova I. (2006): Diversity of wetland vegetation in the Bulgarian high mountains, main gradients and context-dependence of the pH role. – Plant Ecol. 184: 111–130.

Hájková P., Hájek M., Apostolova I., Zelený D. & Dítě D. (2008): Shifts in the ecological behaviour of plant species between two distant regions: evidence from the base richness gradient in mires. – J. Biogeogr. 35: 282–294.

Hájková P., Wolf P. & Hájek M. (2004): Environmental factors and Carpathian spring fen vegetation: the importance of scale and temporal variation. – Ann. Bot. Fenn. 41: 249–262.

Hegedüšová K. (2007): Centrálna databáza fytocenologických zápisov (CDF) na Slovensku [Central database of phytosociological relevés in Slovakia]. – Bull. Slov. Bot. Spol. 29: 124–129.

Hegi G., Merxmüller H. & Reisigl H. (1977): Alpenflora. – Paul Parey, Berlin and Hamburg.

Hrivnák R., Blanár D. & Kochjarová J. (2004): Vodné a močiarne rastlinné spoločenstvá Muránskej planiny [Water and mire plant communities of Muránska planina]. – Reussia 1: 33–54.

Jeník J. (1961): Alpinská vegetace Krkonoš, Králického Sněžníku a Hrubého Jeseníku: teorie anemoorografických systémů [Alpine vegetation of Krkonoše, Králický Sněžník and Hrubý Jeseník: Theory of anemoorographical systems]. – Academia, Praha.

Kliment J., Kochjarová J., Hrivnák R. & Šoltés R. (2008): Spring communities of the Veľká Fatra Mts (Western Carpathians) and their relationship to central European spring vegetation. – Pol. Bot. J. 53: 29–55.

Krajina V. (1933): Die Pflanzengesellschaften des Mlynica-Tales in den Vysoké Tatry (Hohe Tatra). I. Teil. – Beih. Bot. Centralblatt 50: 774–957.

Lamentowicz M., Lamentowicz L., van der Knaap W. O., Gabka M. & Mitchell E. A. D. (2010): Contrasting species-environment relationships in communities of testate amoebae, bryophytes and vascular plants along the fen-bog gradient. – Microbial Ecol. 59: 499–510.

Lexa J., Bezák V., Elečko M., Mello J., Polák J., Potfaj M. & Vozár J. (eds) (2000): Geologická mapa Západných Karpát a priľahlých území [Geological map of West Carpathians and adjacent regions]. – Štátny Geologický Ústav Dyonýza Štúra, Bratislava.

Malmer N. (1986): Vegetational gradients in relation to environmental conditions in northwestern European mires. – Can. J. Bot. 64: 375–383.

Marhold K. & Hindák F. (eds) (1998): Checklist of non-vascular and vascular plants of Slovakia. –Veda, Bratislava.

Marini L., Fontana P., Scotton M. & Klimek S. (2008): Vascular plant and *Orthoptera* diversity in relation to grassland management and landscape composition in the European Alps. – J. Appl. Ecol. 45: 361–370.

Matuszkiewicz W. (2007): Przewodnik do oznaczania zbiorowisk roślinnych Polski [A determination key for plant communities of Poland]. – Pol. Wyd. Nauk, Warszawa.

Molina J. A. (2001): Oligotrophic spring vegetation in Spanish mountain ranges. – Folia Geobot. 36: 281–291.

Nekola J. C. (2004): Vascular plant compositional gradients within and between Iowa fens. – J. Veg. Sci. 15: 771–780.

Nordhagen, R. (1928): Die vegetation und flora des Sylengebietes. – Skr. Nor. Vidensk.-Akad. Oslo. 1:1–612.

Pärtel M. (2002): Local plant diversity patterns and evolutionary history at the regional scale. – Ecology 83: 2361–2366.

Pausas J. G. & Austin M. P. (2001): Patterns of plant species richness in relation to different environments: an appraisal. – J. Veg. Sci. 12: 153–166.

Pawlowski B., Sokolowski M. & Wallish K. (1928): Die Pflanzenassoziationen des Tatra-Gebirges. Teil 7. Die Pflanzenassoziationen und die Flora des Morskie Oko Tales. – Bull. Acad. Polon. Sei. Lett., Cl. Sci. Math. Natur., Ser. B, Sci. natur. 2: 197–272.

Prach K., Košnar J. & Klimešová J. (2010): High Arctic vegetation after 70 years: a repeated analysis from Svalbard. – Polar Biol. 33: 635–639.

Rodwell J. S., Schaminée J. H. J., Mucina L., Pignatti S., Dring J. & Moss D. (2002): The diversity of European vegetation. An overview of phytosociological alliances and their relationships to EUNIS habitats. – Rapport EC-LNV 2000/054. Wageningen.

Rosenzweig M. L. (1995): Species diversity in space and time. – Cambridge University Press, Cambridge.

Rybníček K., Balátová-Tuláčková E. & Neuhäusl R. (1984): Přehled rostlinných společenstev rašelinišť a mokřadních luk Československa [Survey of the plant communities of bogs and wet meadows in Czechoslovakia]. – Studie ČSAV, Praha.

Šály R. & Šurina B. (2002): Soils. – In: Miklós E. (ed.), Landscape atlas of the Slovak Republic, Ed. 1, p. 105–111, Ministry of Environment of the Slovak Republic, Slovak Environmental Agency, Banská Bystrica.

Sekulová L. & Hájek M. (2009): Diversity of subalpine and alpine vegetation of the eastern part of the Nízke Tatry Mts in Slovakia: major types and environmental gradients. – Biologia 64: 908–918.

Šibík J., Kliment J., Jarolímek I., Dúbravcová Z., Bělohlávková R. & Paclová L. (2006): Syntaxonomy and nomenclature of the alpine heaths (the class *Loiseleurio-Vaccinietea*) in the Western Carpathians. – Hacquetia 5: 37–71.

Sillinger P. (1933): Monografická studie o vegetaci Nízkych Tater [Monography about vegetation in Nízke Tatry Mts]. – Slovanský ústav, Praha.

Sjörs H. (1952): On the relation between vegetation and electrolytes in north Swedish mire waters. – Oikos 2: 241–258.

Sjörs H. & Gunnarsson U. (2002): Calcium and pH in north and central Swedish mire waters. – J. Ecol. 90: 650–657.

Šoltés R., Hájek M. & Valachovič M. (2001): *Oxycocco-Sphagnetea.* – In: Valachovič M. (ed.), Rastlinné spoločenstvá Slovenska 3. Vegetácia mokradí [Plant Communities of Slovakia 3. Vegetation of Wetlands], p. 275–296, Veda, Bratislava.

Spitale D., Petraglia A. & Tomaselli M. (2009): Structural equation modelling detects unexpected differences between bryophyte and vascular plant richness along multiple environmental gradients. – J. Biogeogr. 36: 745–755.

Šrůtek M. & Doležal J. (2003): Functional interdependence between climatic factors, topographic processes and spatial patterns of species richness in mountain areas: a special case or the general pattern? – Biologia 58: 823–832.

Steiner G. M. (1992): Österreichischer Moorschutzkatalog. 4. Aufl. – Verlag Ulrich Moser, Graz.

Steiner G. M. (1993): *Scheuchzerio-Caricetea fuscae.* – In: Grabherr G. & Mucina L. (eds), Die Pflanzengesellschaften Österreich II, p. 402–446, Gustav Fischer Verlag, Jena.

Strohbach M., Audorff V. & Beierkuhnlein C. (2009): Drivers of plant species composition in siliceous spring ecosystems: groundwater chemistry, catchment traits or spatial factors? – J. Limnol. 68: 375–384.

Szafer W., Pawłowski B. & Kulczyński S. (1923): Die Pflanzenassoziationen des Tatra-Gebirges. I. Teil. Die Pflanzenassoziationen des Chochołowska-Tales. – Bull. Acad. Polon. Sci. Lett., cl. math.-natur., Sect. B, 1–66.

Tahvanainen T. & Tuomaala T. (2003): The reliability of mire water pH measurements: a standard sampling protocol and implications to ecological theory. – Wetlands 23: 701–708.

Tichý L. & Chytrý M. (2006): Statistical determination of diagnostic species for site groups of unequal size. – J. Veg. Sci. 17: 809–818.

Tichý L., Hájek M. & Zelený D. (2010): Imputation of environmental variables for vegetation plots based on compositional similarity. – J. Veg. Sci. 21: 88–95.

Valachovič M. (ed.) (2001): Rastlinné spoločenstvá Slovenska 3. Vegetácia mokradí [Plant Communities of Slovakia 3. Vegetation of Wetlands]. – Veda, Bratislava.

Valachovič M. & Janovicová K. (1999): Altitudinal differentiation of oligotrphic water-spring vegetation in Slovakia. – Thaiszia – J. Bot. 9: 49–62.

Vanderpoorten A. & Engels P. (2003): Patterns of bryophyte diversity and rarity at a regional scale. – Biodiv. Cons. 12: 545–553.

Vitt D. H. & Belland R. J. (1997): Attributes of rarity among Alberta mosses: patterns and predictions of species diversity. – Bryologist 100: 1–12.

Vitt D. H., Li Y. & Belland R. J. (1995): Patterns of bryophyte diversity in peatlands in continental western Canada. – Bryologist 98: 218–227.

Vonlanthen C. M., Kammer P. M., Eugster W., Bühler A. & Veit H. (2006): Alpine vascular plant species richness: the importance of daily maximum temperature and pH. – Plant Ecol. 184: 13–25.

Wamelink G. W. W., Joosten V., van Dobben H. F. & Berendse F. (2002): Validity of Ellenberg indicator values judged from physico-chemical field measurements. – J. Veg. Sci. 13: 269–278.

Weber H. E., Moravec J. & Theurillat J.-P. (2000): International Code of Phytosociological Nomenclature, Ed. 3. – J. Veg. Sci.1: 739–768.

Wilson S. D. & Nilsson C. (2009): Arctic alpine vegetation change over 20 years. – Glob. Change Biol. 15: 1676–1684.

Zechmeister H. & Mucina L. (1994): Vegetation of European springs: high-rank syntaxa of the *Montio-Cardaminetea*. – J. Veg. Sci. 5: 385–402.

Received 6 September 2010
Revision received 8 December 2010
Accepted 15 December 2010