Patterns of bryophyte and vascular plant richness in European subalpine springs

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Abstract The diversity of spring habitats can be determined not only by local environmental conditions, but also by large-scale biogeographical effects. The effects can differ across various groups of organisms. We compared α-, β- and γ-diversity patterns of bryophytes and vascular plants of (sub)-alpine springs in three contrasting mountain ranges: Alps (Switzerland), Balkans (Bulgaria), Western Carpathians (Slovakia, Poland). We used univariate and multivariate statistics to test for the effects of pH, conductivity, altitude, slope, mean annual temperature and annual precipitation on diversity patterns of both taxonomic groups and compared diversity patterns among the regions for particular pH and conductivity classes. We identified acidophyte and basiphyte, calcifuge and calcicole species using species response modelling. All regions displayed significant relationship between conductivity and α-diversity of vascular plants. Bulgaria showed the highest α-diversity of vascular plants for the middle part of the conductivity gradient. For both taxonomic groups, the β-diversity in the middle part of gradient was highest in Swiss Alps. The total species pool was lowest in Bulgaria. The percentage of basiphyte and calcicole species was highest in the Alps. In (sub)alpine springs, mineral richness was a better determinant of vascular plant α-diversity than pH, and the extent of the alpine area did not coincide with α-diversity. Observed inter-regional differences in diversity patterns could be explained by the different proportion of limestone bedrock and different biogeographic history. The

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differences in α-diversity between both taxonomic groups are presumably result of the different rates of adaptation processes.

Introduction

Variation in species richness has long attracted the interest of ecologists. Water pH and mineral richness are well known as major determinants of wetland plant diversity and composition (Glaser et al. 1990; Tahvanainen 2004; Hájková et al. 2006; Strohbach et al. 2009; Sekulová et al. 2011; Tomaselli et al. 2011). However, few studies focused on (sub)alpine springs. Even if springs are usually small-sized, they inhabit a great diversity of organisms (e.g. Cantonati et al. 2006; Virtanen et al. 2009). In contrast to other plant communities, the species composition of springs is similar over wide areas (Strohbach et al. 2009), which facilitates the direct comparisons. In addition, ecological studies in springs have the advantage that their areas are clearly differentiated from the surrounding habitats, in particular with a constant presence of water, low temperature fluctuations and nutrient limitation (Cantonati et al. 2006). Further, the spring diversity is, generally, also controlled by environmental factors such as hydrological and thermal stability as well as the high oxygen saturation of water, high air humidity and relatively mild winter conditions compared to the surrounding (Spitale et al. 2009). The springs can also be helpful in answering questions about differences between bryophytes and vascular plant diversity in response to environmental gradients (e.g. Spitale et al. 2009), because both taxonomic groups are abundant and often strong competitors in springs (During and Van Tooren 1990; Bergamini and Peintinger 2002), but they differ in important traits such as nutrition or dispersal ability (Spitale et al. 2009; Hájek et al. 2011).

Spring diversity patterns can be further explained by using the species pool concept (Pärtel et al. 1996; Zobel et al. 1998) supposing that local diversity critically depends on a number of species which occur in a given region and simultaneously are adapted to grow in a target habitat. Some recent studies have suggested that this species pool effect is closely related to the proportion and total area of particular habitats (Pärtel 2002; Hájek et al. 2007; Chytrý et al. 2010)— the more time a particular habitat type or suite of environmental conditions has persisted and the more common it has been geographically, the greater the opportunity for the evolution of a pool of suitably adapted species or ecotypes. Thus, the diversity of spring habitats can be determined not only by local environmental conditions, but also by the species pool size of both vascular plants and bryophytes. To test these effects, it is worth exploring the diversity patterns of (sub)alpine springs in a wide set of study regions, differing mutually in total mountain area and representation of particular habitats.

Therefore, we compared diversity patterns in (sub)alpine springs in three contrasting European high mountain regions: Swiss Alps, Bulgarian high mountains and Western Carpathians in terms of different components of diversity. For defining these components we used classical concepts of α-, β- and γ-diversity (Whittaker 1960). α-Diversity refers to local diversity, most often to the number of species in the sampling plot. β-Diversity is understood in different ways across the studies (e.g., Tuomisto 2010); in this study we understand β-diversity as non-directional variation in community structure among vegetation plots within a given region (Anderson et al. 2011). γ-Diversity is defined as the regional species pool, i.e. as the set of species in each region which are capable to occur in a target community (Pärtel et al. 1996). It can be, together with the α-diversity, viewed as inventory diversity (Jurasinski et al. 2009), which is basically the same concept being different only by the scale.

Our research questions are:

(i) Which ecological factors (water pH, conductivity, altitude, slope) are related to the α-diversity of springs in particular regions, and can some general patterns be detected?

(ii) Do α-, β- and γ-diversity differ among mountain ranges of different areas and thereby a different proportion of spring habitats?

(iii) Are diversity patterns concordant between vascular plants and bryophytes and among the range of pH observed?

(iv) Is the different representation of calcareous bedrock in particular regions reflected in the ratio between calcifuge and calcicole species?

Methods

Study area

We investigated springs located in three contrasting European high mountain ranges: the Swiss Alps, Western Carpathians and Bulgarian mountains (Fig. 1). All study sites were located within the subalpine and low alpine zone. The total area of alpine habitats in the study regions decreased from the Swiss Alps through Bulgaria to the Western Carpathians. The climate of these high mountains is cold and humid, consisting of short, wet summers and cold winters. The mean precipitation in the (sub)alpine zone is usually more than 1200 mm in Western Carpathians and Swiss Alps and more than 700 mm in Bulgaria with mean annual temperature about zero (Federal Office of Meteorology and Climatology MeteoSwiss, SHMU— Slovak Hydrometeorological Institute, Lieth et al. 1999). For example, at Gütch ob Andermatt (2287 m) in the Swiss Alps the annual mean temperature (1961–1990) is −0.5°C with a 1479 mm mean year precipitation. At Chopok (2005 m) in the Western Carpathians, the annual mean temperature (1955–2007) is −1.1°C with a 1090 mm mean year precipitation and at the Botev peak (2376 m) in Bulgaria, the annual mean temperature (1963–1990) is −0.2°C with a mean year precipitation of 960 mm. The highest parts of all studied mountains were strongly influenced by the Pleistocene glaciers. The bedrock of studied mountains in the Western Carpathians (Vysoké Tatry, Západné Tatry, Belianske Tatry, Nízke Tatry, Malá Fatra) is with the exception of the eastern part of the Nízke Tatry Mts and Belianske Tatry mostly 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 and Šurina 2002). A nappe built from limestone and shale can be found, but it rarely reaches the subalpine zone. 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) and Belianske Tatry of limestones. At high altitudes of studied sites in Bulgaria (Stara planina,

Rila, Pirin), the acidic bedrock prevails. Rila (2925 m) and Pirin (2915 m) Mts are the highest mountains in the Balkan Peninsula and the whole area is rich in springs and streams. Crystalline rocks prevail here (Cheshitev and Kanchev 1989). The northern part of the Pirin Mt (Vihren peak) is constituted of marbles, but this area is very dry and poor in spring habitats. The geological structure of Stara planina Mt is rather complicated and connected with multifarious relief (Hájková et al. 2006). Nevertheless, the regions with the occurrence of (sub)alpine springs and mires are located mostly on siliceous bedrock (granodiorites). The calcium-rich bedrock is much more frequent in the Alps than in the other two regions and crystalline rocks are often mixed with calcareous rocks. The Pennine Alps have a complicated geology. They consist of shists, gneisses intruded by granites, phyllites, amphibolites and limestones (Swisstopo 2005). Bernese, Urnese and Glarus Alps are build mainly of ophiolites, limestone, marble, gneisses, schists, amphibolites and granite intrusions. Lepontine Alps are partly built of limestones and ophiolites and partly of metamorphic rocks such as phyllites and schists.

Data collection

We sampled 177 vegetation plots (4 × 4 m^2) within the rheocrene or helocrene springs (one plot per spring) above the tree line (1500–2000 m a.s.l.). If springs were smaller in size, we sampled their full areas (see Table 1 for further details). We included 13 vegetation plots from existing studies (Schubiger-Bossard 1988; Steiner 2002) from Swiss Alps, which were supplemented only with pH, altitude, slope orientation and coordinates, but lacking conductivity values. With each vegetation plot some environmental variables: water pH, conductivity, altitude and slope were recorded. The pH and conductivity were measured in situ directly in the spring water. If the water table was below the surface of moss layer a small shallow pit was dug and the water in the pits was let to settle down before measurements. Both factors were standardised at 20°C. Conductivity caused by hydrogen ions was subtracted. Corrected conductivity was used as a proxy for the total mineral richness of the water, correlating most strongly with the sum of calcium and magnesium concentrations (Sjörs and Gunnarsson 2002). Altitude was measured with a GPS receiver (Garmin GPSmap 60CSx) in the field. Mean
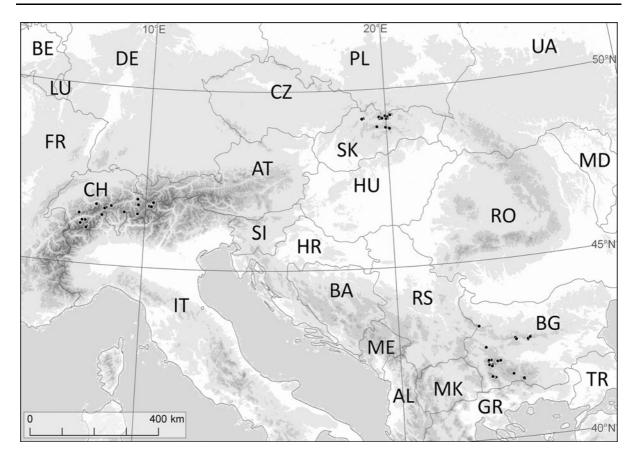
Fig. 1 The location of vegetation plots in the study regions. The country codes are indicated

annual temperature and annual precipitation were taken from a climatic model with 1 km resolution (Hijmans et al. 2005). Descriptive statistics of variables gathered with the vegetation plots was summarised in Table 1. All vascular plants and bryophytes were identified and their cover was estimated using the nine-grade cover scale (Van der Maarel 1979). The nomenclature of the taxa follows the Checklist of Nonvascular and Vascular Plants of Slovakia (Marhold and Hindák 1998); the nomenclature of the taxa not included in this checklist follows Lauber and Wagner (2007) and Kozhuharov (1992).

Data processing

Environmental variables were tested for normality of distribution via a chi-square test using the STATIS-TICA 9 program (version 9.0, StatSoft Inc., 261 Tulsa), with variables having non-normal, right-skewed distributions log-transformed prior to analysis.

Although species counts were not significantly ($P < 0.05$) correlated with log plot size in most of the cases (except for bryophytes in Swiss Alps) and the measured environmental factors were not correlated with plot size, we removed any possible effect of unequal plot sizes by calculating linear regressions of the local α-diversity (species counts) on log-transformed plot size (e.g. Chytrý et al. 2003). A logarithmic transformation was used to fit the empirical species-area relationship (Rosenzweig 1995). In further analyses, we used α-diversity controlled for log-transformed plot size by taking standardised residuals of this regression instead of species counts.

To determine how α-diversity is related to environmental factors, polynomial regression models built by means of a backward stepwise selection of variables were created separately for vascular plants and bryophytes in all three study regions using STATISTICA program.

Table 1 Descriptive statistics of the vegetation plot characteristics

	Mean	Min.	Max.	SD
Swiss Alps				
Vegetation plot area	11.9	4	16	4.7
Altitude	2257.9	1924	2762	189.0
Slope inclination	7.3	0	45	9.9
pH	7.2	4.6	8.6	0.9
Conductivity	166.6	14.7	642.0	141.1
Mean January temperature	−7.2	−9.6	−5.6	0.9
Mean June temperature	8.0	4.5	10.4	1.3
Mean annual temperature	0.03	−3.1	2.1	1.1
Annual precipitation	1694.1	1156	2080	287.2
W. Carpathians				
Vegetation plot area	11.0	4	16	4.6
Altitude	1621.2	1330	2005	143.7
Slope inclination	12.3	0.0	45.0	11.5
pH	6.6	4.9	8.5	0.9
Conductivity	80.3	7.0	335.0	93.6
Mean January temperature	−8.0	−8.7	−7.1	0.4
Mean June temperature	9.4	7.4	11.9	1.1
Mean annual temperature	0.9	−0.7	3.0	0.8
Annual precipitation	1421.4	1236.0	1642.0	109.6
Bulgarian Mts				
Vegetation plot area	10.5	4	16	4.3
Altitude	2083.0	1367	2493	264.5
Slope inclination	13.4	0	40	11.2
pH	6.6	5.3	8.3	0.6
Conductivity	40.6	8.0	203.0	39.0
Mean January temperature	−7.1	−8.5	−5.1	0.7
Mean June temperature	10.0	7.7	14.5	1.4
Mean annual temperature	1.5	−0.7	5.2	1.2
Annual precipitation	756.9	684.0	844.0	47.8

To reveal intra-regional differences in α- and β-diversity along the pH and conductivity gradients, we allocated the vegetation plots into three arbitrarily defined pH and conductivity classes (pH: <6, 6–7, >7; conductivity <50, 50–100, >100 μS cm^{-1}; Appendix 1 in Supplementary material). The list of acidophyte, basiphyte, calcifuge and calcicole species is summarised in Appendix 2 in Supplementary material.

β-Diversity among the a priori groups (comparing the three pH or conductivity classes in three regions) was calculated using the permutational analysis of multivariate dispersions (PERMDISP; command 'betadisper' from the 'vegan' package; Anderson 2006; Anderson et al. 2006; Oksanen et al. 2010) and Bray–Curtis distance matrices. Since Bray–Curtis dissimilarity is not Euclidean (Legendre and Gallagher 2001), Principal Coordinate Analysis is used to place the observations into an Euclidean space. Multivariate dispersion is the average dissimilarity of each plot to the centroid of a defined group of plots in multivariate space; i.e. larger distance to centroid means larger β-diversity. The same approach, advocated by Anderson et al. (2011), was used, for example, by Bunn et al. (2010) and Taft et al. (2011). The analysis was computed in R software (R Development Core Team 2010).

The significance of differences between the three regions in particular pH or conductivity classes was tested using Tukey's post hoc tests.

The differences in γ-diversity (regional species pool, i.e. the number of species in each region capable to occur in a spring community) were compared using sample-based rarefaction curves (Gotelli and Colwell 2001). These curves were computed from the means of 1000 sample-based species accumulation curves that were calculated from random ordering of all plots in particular region. They illustrate how the cumulative number of all species increases with increasing number of sampled plots. Rarefaction curves were computed using the JUICE program (Tichý 2002).

We further investigated the relative number of acidophyte, basiphyte, calcifuge and calcicole species in each region to determine if the distribution of the particular species was related to the proportion of habitats as predicted by the species pool hypothesis. To designate species as acidophyte or basiphyte, we created species response curves to pH in R software (R Development Core Team 2010) using the Generalised Additive Models (library 'mgcv', Wood 2006) with automatic selection of degrees of freedom based on the Akaike information criterion. The same approach was used to determine calcicole and calcifuge species. In this case we created species response curves to water conductivity. Only species with more

than ten occurrences were analysed. The particular species was designated as basiphyte if the species optimum was greater than pH 7, as neutral if a species optimum was in pH between 6 and 7 and as acidophyte if the species optimum was lower than pH 6. Concerning water conductivity, the threshold values were defined as lower than 50 (calcifuge species; species with optimum in mineral-poor springs), between 50 and 100 (intermediate species; species with optimum in mineral moderately rich springs) and over 100 $\mu S\ cm^{-1}$ (calcicole species; species with optimum in mineral extremely rich springs).

Results

α- and γ-Diversity pattern

We found 262 plant species in (sub)alpine springs in the Swiss Alps, 264 in the Western Carpathians and 190 in the Bulgarian mountains. Detailed information can be found in Table 2. All three regions showed a significant linear or unimodal relationship between conductivity and α-diversity of vascular plants and except for Swiss Alps of bryophytes (Table 3). α-Diversity of vascular plants further showed significant relationships to pH in the Western Carpathians and to altitude in the Swiss Alps and Bulgaria. The α-diversity of bryophytes was significantly correlated with inclination in W. Carpathians, annual precipitation in Bulgarian Mts and in Swiss Alps none of the factors was significant.

When particular pH and conductivity classes (Fig. 2) were analysed separately, only significant differences in α-diversity of vascular plants related to pH were found in Western Carpathians; the alkaline springs were more species rich than acidic ones. α-Diversity of vascular plants was clearly more influenced by conductivity than pH and we found significant differences in all studied regions. However, the particular patterns differed. The relationship between conductivity and bryophytes was more consistent; the alkaline springs in Western Carpathians and Bulgaria were significantly less species-rich than the acidic ones. In Swiss Alps, the highest α-diversity of bryophytes was found in the middle part of the conductivity gradient.

γ-Diversity was similar in the Swiss Alps and the Western Carpathians, but lower in Bulgaria (Fig. 3).

β-Diversity pattern

The overall β-diversity of bryophytes did not show any differences among the regions, the overall β-diversity of vascular plants was highest in Swiss Alps and lowest in Western Carpathians (Fig. 4). The β-diversity pattern further differed among the pH classes (Fig. 5). In the middle part of the gradient, the β-diversity of vascular plants in Western Carpathians was lower than in Bulgarian Mts and Swiss Alps, the β-diversity of bryophytes was higher in Swiss Alps than in Carpathians. In the acidic part of the gradient, the Western Carpathians showed greater β-diversity of bryophytes than Swiss Alps.

Acidophyte and basiphyte species

The relative number of basiphyte and calcicole species in springs was highest in the Swiss Alps (Table 4). In the Western Carpathians, we found the highest relative number of acidophyte species and in Bulgaria the highest relative number of neutral pH species and lowest relative number of basiphyte species. In

Table 2 Descriptive statistics of the total number of inventoried species in springs in the three study regions

Region	Plots	All species			Vascular plants			Bryophytes		
		No.	Mean	SD	No.	Mean	SD	No.	Mean	SD
Swiss Alps	27	262	25.0	9.3	177	17.4	8.1	85	7.6	4.5
W. Carpathians	31	264	22.2	6.5	163	14.2	8.0	101	8.0	3.8
Bulgarian Mts	20	190	17.3	8.8	137	13.3	7.0	53	4.1	2.1

Only vegetation plots of 16 m^2 are considered

No. total number of species found in springs in a given region (regional species pool), *Mean* mean number of species per vegetation plot

Table 3 Results of polynomial regression models built by means of a backward stepwise selection of variables testing separately the relationships between α-diversity controlled for log-transformed plot size and environmental factors for bryophytes and vascular plants

	Swiss Alps		W. Carpathians		Bulgaria	
	Vascular plants	Bryophytes	Vascular plants	Bryophytes	Vascular plants	Bryophytes
Altitude	10.29**	n.s.	n.s.	n.s.	7.43**	n.s.
Altitude2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Inclination	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Inclination2	n.s.	n.s.	n.s.	10.70**	n.s.	n.s.
pH	n.s.	n.s.	6.47*	n.s.	n.s.	n.s.
pH2	n.s.	n.s.	7.98**	n.s.	n.s.	n.s.
Conductivity	n.s.	n.s.	n.s.	n.s.	12.24***	5.70*
Conductivity2	7.51**	n.s.	5.60*	11.41**	8.73**	4.90*
Mean annual temperature	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mean annual temperature 2	n.s.	n.s.	6.48*	n.s.	n.s.	n.s.
Annual precipitation	n.s.	n.s.	7.55**	n.s.	n.s.	n.s.
Annual precipitation2	n.s.	n.s.	7.68**	n.s.	n.s.	6.09*
R^2 adj. of the model	0.33	–	0.22	0.18	0.36	0.14

The variance accounted for by the whole regression model is presented as the adjusted R^2 statistics. F values are presented

Variable linear relationship, *Variable2* unimodal relationship, *n.s.* non-significant

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Bulgaria, we found approximately equal number of calcifuge and calcicole species.

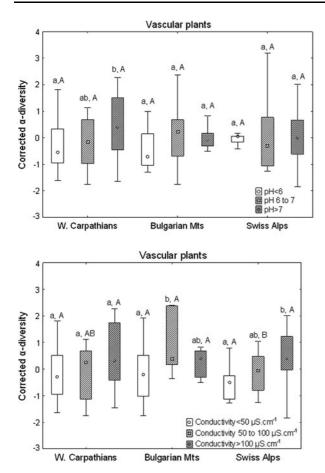## Discussion

Determinants of α-diversity

Contrary to the studies showing a strong relationship between plant richness and pH (e.g. Glaser et al. 1990; Hájková and Hájek 2003), pH was important only for determining of vascular plant α-diversity in the Western Carpathians. The lack of a relationship between α-diversity and pH in the (sub)alpine springs of the Alps and Bulgaria confirms and enlarges the result reported from Bulgaria by Hájková et al. (2006). It seems to be of more general validity that a tight correlation between pH, mineral richness and plant α-diversity, so often found in low-altitude wetlands, is reduced to the correlation between mineral richness and plant α-diversity in (sub)alpine springs. Tyler (2003) explains low plant species richness of temperate habitats by a low number of species that are adapted to tolerate much aluminium or hydrogen ions in acidic soils. However, in spring habitats with running water, pH does not drop below the value

ca. 4.5, the threshold when solid aluminium rapidly solubilises and occurs in toxic forms. The results of increasing species richness with increasing mineral richness (approximated by water conductivity) but not pH draws an attention to other possible stressors in mineral-poor wetlands such as iron toxicity or low concentrations of calcium, magnesium, potassium or nitrates (Rozbrojová and Hájek 2008). In alpine springs on crystalline bedrock, these stressors might be more pronounced because of extremely low calcium richness and limited nutrient and mineral input from the surroundings.

The monotonically decreasing α-diversity of vascular plants with increasing altitude as we found in Swiss Alps and Bulgaria is a common pattern in alpine regions at various scales (Rahbek 1995; Körner 2002; Mallen-Cooper and Pickering 2008). Solely in the Western Carpathians, the α-diversity of vascular plants showed no relationship to altitude, probably because of the relatively small altitudinal differences combined with high topographic heterogeneity occurring at a small scale.

The Alps as a whole doubtless harbour more species than smaller mountain ranges, but this effect is less pronounced in local diversity of small-sized springs. Even though the size of the species pool was

Fig. 2 α-Diversity pattern in spring vegetation in the three study regions and for the three different pH classes and conductivity classes. The α-diversity is controlled for log-transformed plot size. *Boxes* and *whiskers* show medians and 50 and 95%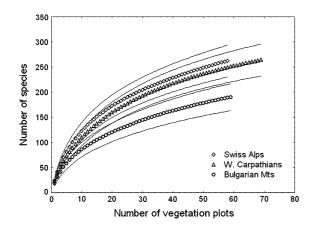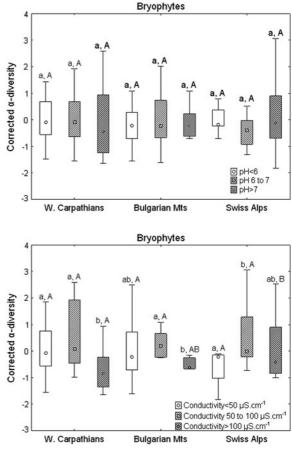 percentiles. Significant differences among regions ($P < 0.05$, Tukey's post hoc test) are marked by letters *A*, *B* and among particular classes within region by letters *a*, *b*

Fig. 3 Sample-based rarefaction curves of the number of species (bryophytes and vascular plants together). 95% confidence interval is shown

lowest in Bulgaria, this difference did not significantly affect the local α-diversity. An explanation could be the existence of assembly rules driven by the competitive exclusion of incidental species that maintain similar local α-diversity despite differences in the species pool size. Study scale is an important factor that drives relationships between local α-diversity and species pool (Koleff and Gaston 2002; Dufour et al. 2006) and thereby the small area of springs might deepen the competitive exclusion and might be therefore responsible for our result. Our result supports the view that inherent linear or curvilinear relationships between local α-diversity and the size of regional species pool (Fox and Srivastava 2006) might not be always manifested (Akatov et al. 2005).
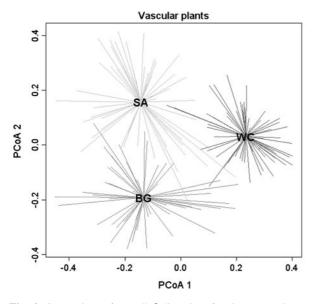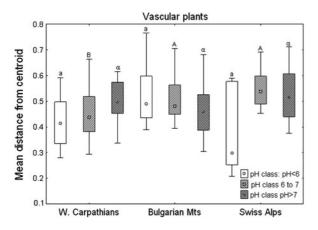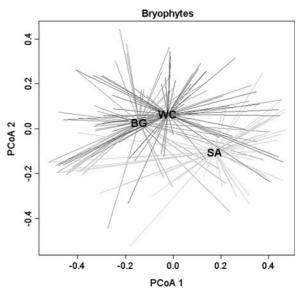
Fig. 4 Comparison of overall β-diversity of spring vegetation in the three study regions for vascular plants and bryophytes. β-Diversity (dispersion of groups) of vascular plants was highest in Swiss Alps and lowest in Western Carpathians while no difference was found for bryophytes (ANOVA and subsequent Tukey's post hoc test). *BG* Bulgarian mountains, *SA* Swiss Alps, *WC* Western Carpathians
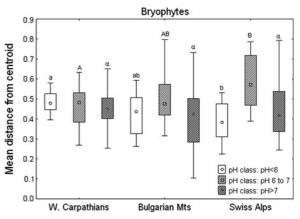

Fig. 5 Comparison of beta diversity of spring vegetation in the three study regions across different pH classes and for vascular plants and bryophytes. Higher values of mean Bray–Curtis distance from centroid indicate higher beta diversity. *Boxes* and *whiskers* show medians and 50 and 95% percentiles. Significant differences among regions (Tukey's post hoc test) are marked by letters (*a*, *b*, *A*, *B*, α)

Vascular plants versus bryophytes

Our study demonstrates the different pattern of vascular plants and bryophyte species richness along environmental gradients in particular regions. In Bulgaria, vascular plant assemblages of moderately mineral-rich springs are enriched by Balkan endemics and species with a regionally shifted realised niche, while few shifts in realised niches and no endemic species were found in the case of bryophytes (Hájková et al. 2006, 2008). Bryophytes, generally, form more similar assemblages across distant regions than do vascular plants and even exhibit many intercontinental distributions, probably resulting from long-distance dispersal which enlarges species distribution ranges and, in addition, maintains gene flow (Szövényi et al. 2008; Vanderpoorten et al. 2008) and thus probably prevents local adaptations into ecotypes. The different

Table 4 The percentage of plant species with response optimum in acidic (pH < 6), neutral (pH 6–7) and alkaline (pH > 7) springs (acidophyte, neutral and basiphyte species) and in mineral-poor (conductivity < 50 μS cm^{-1}), mineral- rich (conductivity 50–100 μS cm^{-1}) and extremely mineral-rich water (conductivity > 100 μS cm^{-1}) (calcifuge, intermediate and calcicole species) in the three different regions

Region	pH				Mineral richness			
	N	% Acidophyte	% Neutral	% Basiphyte	N	% Calcifuge	% Intermediate	% Calcicole
Swiss Alps	58	28.9	6.7	64.4	47	8.8	5.9	85.3
W. Carpathians	69	33.3	22.9	43.8	69	28.9	18.4	52.6
Bulgarian Mts	59	25	32.5	42.5	59	47.5	12.5	40

Only species with more than 10 occurrences were analysed

N the number of vegetation plots supplemented with measured conductivity or pH

pattern in bryophyte and vascular plant α-diversity across regions could be therefore partially explained by the different nature and rate of adaptation processes in these two different groups of organisms.

The patterns in β-diversity differed between bryophytes and vascular plants. Many studies have found differences in vascular plant and bryophyte richness pattern (Bruun et al. 2006; Grau et al. 2007; Spitale et al. 2009). Spitale et al. (2009) even demonstrated that apparent similarities in the patterns of bryophyte and vascular plant richness could be induced by different environmental variables. Most often, the different responses of bryophytes to mineral richness are explained by different physiologies and life forms (Bragazza and Gerdol 2002; Spitale et al. 2009). The differences in overall β-diversity patterns, caused by both habitat heterogeneity and spatial effects together (Soininen et al. 2007), could be explained either by the different number of specialists within particular groups of organisms or different dispersal ability. The more specialists occurring in a group of species, the higher β-diversity is observed (Jankowski et al. 2009). By contrast, better dispersal ability means lower β-diversity (Qian 2009). In our study, we would expect both processes. On the one hand, bryophytes are well-adapted to dispersal because of microscopic wind-dispersed spores and the generally rich production of propagules (Frahm 2008) but, on the other hand, there is a great level of specialisation within bryophytes (Virtanen et al. 2009). Anyway, bryophyte dispersal ability is much better than the dispersal ability of vascular plants. In the Western Carpathians, Hájek et al. (2011) found that the assemblages of vascular plants were nearly three times more spatially structured than that of bryophytes, whose spatial

structure was even similar to the spatial structure of microscopic diatoms. Better dispersal ability is therefore the most probably responsible for no difference in the β-diversity of bryophytes among the regions.

Acidophyte versus basiphyte species

Our results show that in (sub)alpine springs the percentage of basiphyte and calcicole species is higher than that of acidophyte and calcifuge species, which supports the general assumption that temperate floras have greater numbers of calcicole than calcifuge species because of historical reasons (Pärtel 2002). The majority of alpine species are adapted to calcareous soils, while adaptation to acidic soils might be of more recent evolutionary origin (Conti et al. 1999) and, in addition, calcicole species were favoured during glacial periods in most regions (Ewald 2003). The weaker differentiation between calcicole and calcifuge species in Bulgaria was largely caused by previously described shifts or extensions of realised niches of calcicole species towards more acidic conditions, explained by isolated acidic refugia during dry pleniglacials (Hájková et al. 2008). Such a fast adaptation of the local population of calcicole fen species to acidic conditions could occur only if the gene flow connection to the original calcicole population was interrupted and if populations were abundant and sufficiently genetically diverse (cf. Kirkpatrick and Barton 1997). It is therefore possible that such adaptations did not take place in the other regions, but further evidence from transplantation experiments or genetics is needed. Nevertheless, we indeed found the difference in the representation of calcicole species, mostly those typical of calcareous

fens, which entered springs in the limestone parts of the Swiss Alps, but acidic to neutral springs in Bulgaria. They are rare in Western Carpathian subalpine calcareous springs despite their high abundance below the tree line.

Conclusions

We can conclude that the total mineral richness is a better determinant of vascular plant α-diversity than pH in (sub)alpine springs. We found certain differences in the α-diversity of springs among the regions, which can be related to historical effects connected with a high representation of calcareous substrate in the Swiss Alps and acidic substrate in the Bulgarian high mountains. Our study further demonstrates the different responses of vascular plant and bryophyte diversity to environmental gradients. Finally, we showed that in (sub)alpine springs the percentage of calcicole and basiphyte species is much higher than that of calcifuge and acidophyte species; and the proportion of calcicole species is highest in the Alps with the most abundant calcareous bedrock in the alpine zone. Because diversity patterns across environmental gradients differ among contrasting mountain ranges, it is difficult to find general patterns. It is therefore worth conducting more regional studies focusing on diversity determinants within springs in different regions, as well as on genetic and functional aspects of diversity.

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