

Variability and classification of Carpathian calcium-rich fens: breaking the state borders

Variabilita a klasifikace karpatských vápnatých slatiniš : boření státních hranic

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Calcareous and rich fens harbour the unique biodiversity of plants and invertebrates. They are extremely sensitive to landscape changes because of their island nature. In the Carpathians, they are still well-preserved, but their number has substantially decreased. Knowledge about their variability and classification into vegetation units, a baseline for efficient nature conservancy, is still insufficient in the Eastern Carpathians, where phytosociology has used different methodologies than in the Western Carpathians. It has resulted in artificial boundaries in the distribution of vegetation types and low compatibility with modern European habitat classification schemes. Here we gathered a large set of vegetation-plot records, sampled by the unified sampling protocol. The aim was to uncover the principal variation in compositional data, identify resulting clusters with the hitherto reported vegetation units, and create the unified classification system adjusted for the entire Carpathian territory. In line with previous ecological studies, the unsupervised classifications (Twinspan, beta-flexible clustering method) largely mirrored the base saturation gradient and distinguished between relict fens and younger fen grasslands. We defined formally the cores of 10 vegetation units well reproduced by unsupervised classifications and used them as prototypes in semi-supervised k-means clustering. The final 10 clusters essentially correspond with phytosociological associations, with five of them being reported for the first time for Romania. These vegetation units were well-separated in the principal coordinate analysis, whose first axis separated relict fens from younger fen grasslands, while the second axis followed the water level gradient largely. Groundwater pH and conductivity contributed to forming significant compositional gradients. Climate (temperature, precipitation, number of hot days above 30 °C) and specific edaphic conditions contributed to the diversification of the vegetation types. Our analyses supported the classification of fen grasslands into both the tufa-forming and the peat-forming ones, belonging to different associations and Habitat Directive units, both occurring in all countries including Romania, rather than having a single separate Eastern-Carpathian association. We provide strong evidence for distinguishing the *Sphagno warnstorffii*-*Tomentypnetalia* order and its alliances *Sphagno warnstorffii*-*Tomentypnion nitentis*, *Stygio-Caricion limosae* and *Saxifrago hirculi*-*Tomentypnion* in Romania, the latter missing in other Carpathian countries. The final unified classification system will make Carpathian vegetation types of rich and calcareous fens applicable to continental habitat classification schemes.

Keywords: calcareous fens, *Caricion davallianae*, climate, ecological indicator values, k-means, pH, Poland, Romania, semi-supervised and unsupervised classification, Slovakia, vegetation

Introduction

The minerotrophic calcium-rich fens of the *Caricetalia davallianae* and *Sphagno-Tomentypnetalia* orders represent unique ecosystems with distinct species composition shaped by high groundwater mineralization. Because of their island-like and fragmented nature and a strong dependence on the undisturbed water regime, they are susceptible to any activities in their surrounding like drainage, eutrophication, cessation of mowing or grazing management, water extraction or peat excavation (Pauli et al. 2002, van Diggelen et al. 2006, Mälson et al. 2008, Hájek et al. 2020b). Moreover, ongoing climate change connected with higher temperatures and lower precipitation may disturb the water regime (Weltzin et al. 2003) and negatively influence fen biodiversity. Therefore, minerotrophic calcium-rich fens belong to the most endangered habitats over entire Europe (Janssen 2016, Joosten et al. 2017, Chytrý et al. 2019). In the last decades, many studies focusing on ecological aspects of calcium-rich fens appeared, showing that calcium richness, hydrology, macro-nutrient availability and mowing or grazing management (e.g. Johnson & Steingraeber 2003, Duval & Waddington 2011, Horsáková et al. 2018, Hájek et al. 2020b) are among the most critical environmental drivers. Some studies have demonstrated that the Holocene history of calcium-rich fens may also shape their species composition (Horsák et al. 2012). Old, ancient fens, hereinafter called ‘relict’, initiated in the glacial or Early Holocene times and kept open patches throughout the Middle-Holocene woodland optimum. They have preserved more fen specialists than younger fens that initiated as late as during medieval or post-medieval land use by humans such as deforestation, grazing and mowing (Hájek et al. 2011, Hájková et al. 2020). Classification and syntaxonomical synthesis may bring information on the discrimination of vegetation units and their ecological characteristics and distribution over the study areas. All this information may be helpful in nature conservation as a base for reliable evaluation of calcium-rich fens in Red Lists of habitats and associated conservation schemes.

The Carpathians are a distinct orographic system, the largest one in central-eastern Europe. In this region, a relatively low proportion of fens has been affected by human activities compared to adjacent less elevated areas, still leaving many species-rich sites in a well-preserved state (Šefferová-Stanová 2012, Hájek et al. 2020b). Nevertheless, even here, most current fens are of a small area, and most of them are located in the mountains, whereas sites in lower altitudes mainly were destroyed in the last centuries. The phytosociological research has a long tradition in all Carpathian countries, but critical syntaxonomical syntheses with numerical analyses or formal definitions were carried out only in Slovakia (Dítě et al. 2007), Czech Republic (Hájek & Hájková 2011) and Polish Carpathians (Hájek & Hájková 2002, Koczur & Nicia 2013). In East- and South-Carpathian countries (Ukraine, Romania), national vegetation syntheses do exist as well, but without critical verification of once reported associations in terms of numerical methods or formal definitions (Solomakha 1996, Coldea 1997, Felbaba-Klushyna 2010). The classification used in the latter countries obviously does not stress the compositional differences caused by base saturation and carbonate precipitation, contrary to Western

Carpathians (Hájek 2002, Dítě et al. 2007) or Europe as a whole (Peterka et al. 2017). Notably, the base saturation gradient governs species composition not only of plants but also other groups of organisms (Horsák & Hájek 2003, Opravilová & Hájek 2006, Bojková et al. 2011, Zhai et al. 2015), making it crucial in general classification schemes. Vegetation types distinguished along the gradients of base saturation and calcium carbonate precipitation are well identifiable with European habitat classification systems such as Habitat Directive (Evans 2006) or EUNIS (Chytrý et al. 2020). However, such transferability is not the case of the Eastern and Southern Carpathians, where different classification criteria have been used so far, resulting in separate Western- and Eastern-Carpathian associations whose distribution artificially ends at state borders. The classification system used in Eastern and Southern Carpathians (Romania, Ukraine) follows the original idea of R. Soó (1944, 1947, 1949) to classify all short-sedge fens with cotton grasses (*Eriophorum*) into a single association called *Carici flavae-Eriophoretum* regardless of hydrology, calcium content or carbonate tufa precipitation. Later, Puşcaru et al. (1956) and Coldea (1977, 1997) reported or described the associations characterized by the dominance of *Blysmus compressus*, using successively three similar yet different names, with *Carici flavae-Blysmetum compressi* being used in the last national vegetation survey (Coldea 1997). According to their original diagnoses, these associations occur on mineral soil, but not exclusively tufa-forming wetlands, and sometimes are determined by grazing. In Romania, the dominance of a single species had been a criterion also for delimiting the relict associations dominated by calcicole plants (*Caricetum davallianae*, *Orchido-Schoenetum nigricantis*) or boreal sedges regardless of base saturation. On the contrary, in the Western Carpathians, the compositional variation driven by base saturation, presence of *Sphagnum*, and relictualisms had been more stressed (Hájek et al. 2006, Dítě et al. 2007, Horsák et al. 2007). On the other hand, disturbed fens dominated by a single species are also included in some Western-Carpathian classification systems, but *Eleocharis quinqueflora* dominance had been stressed instead of the dominance of *Blysmus compressus* (Dítě et al. 2007, Hájek & Hájková 2011). As a result, the distribution of the *Carici flavae-Eriophoretum* and *Carici flavae-Blysmetum compressi* associations ends at Romanian and Ukrainian borders. Behind them, the *Carici flavae-Cratoneuretum filicini*, *Valeriano simplicifoliae-Caricetum flavae*, *Campylio-Caricetum lasiocarpae*, and *Eleocharitetum pauciflorae* associations start to occur. Such a pattern would have a scientific background only if some significant geographical gradients connected to biogeography, macroclimate, or cultural differences in human use of fens occur and are equal to or exceeding the other gradients such as tufa precipitation, base saturation or hydrology. Until now, no study has tested this.

The suspicion that the Romanian and Ukrainian classification systems do not capture sufficiently the European habitat classification systems and significant ecological gradients is highlighted by the results of the European synthesis of fen vegetation at an alliance level (Peterka et al. 2017). This synthesis suggests the occurrence of the *Sphagno warnstorffii-Tomentypnion*, *Stygio-Caricion limosae* and *Saxifrago hirculi-Tomentypnion* alliances in this area from which they have never been reported previously. Our study aims to verify their occurrence using the pan-Carpathian data set, present the detailed compositional data, including regionally valid differential and character species, and identify their regional communities with existing associations, or describe the new ones.

The critical vegetation survey of Carpathian calcium-rich fens is not an as easy task as it could seem. Different vegetation science traditions had met in the Carpathian region, resulting in inconsistent methodology and sampling efforts (see Material and methods). To overcome these problems, we accumulated original vegetation-plot records from the entire Carpathian area since 1996 using a unified methodology. Now we came to the stage that we can critically analyse the compositional variation on Carpathian fens in the light of noticeable classification differences among individual countries. We aim to analyse all these vegetation data from the entire Carpathians. We used numerical methods involving unsupervised and semi-supervised techniques to uncover the major variation in compositional data and identify it with the reported vegetation units. Only when we had imaginary broken state borders we can judge which widely reported vegetation types are well-delimited by species composition and ecological conditions and how they are actually distributed. Therefore, this study aims to uncover the principal variation in compositional data, identify resulting clusters with the hitherto reported vegetation units, and create a unified classification system adjusted for the entire Carpathian territory.

Material and methods

Study area

The study area covers almost the entire Carpathian range on the territory of the Czech Republic (CZ), Slovakia (SK), Poland (PL), Ukraine (UA) and Romania (RO). Marginal areas situated in Austria, Hungary and Serbia were not included in our study. The Carpathians form the second largest mountain system in Europe, forming an arc of 1300–1500 km in length and 100–350 km in width. They are divided into the Western Carpathians (Outer and Inner W. Carpathians; CZ, SK, PL), the Eastern Carpathians (PL, UA, RO), the Southern Carpathians (RO) and the Apuseni Mts (RO). Between the Eastern and Southern Carpathians and the Apuseni Mts, there is a Transylvanian Basin, a large inter-mountain hilly basin, sometimes geographically included to the Carpathians (Kondracki 1989). Geologically, peripheral parts of the Western Carpathians and northern part of the Eastern Carpathians are built by flysch nappes with alternating sandstones, limestones and schists, fringed by a narrow limestone Klippen Belt occurring along the entire flysch zone. Other parts of the Carpathians are composed of crystalline or volcanic rocks (granite, locally metamorphic rocks, andesite and other rocks), often with limestone nappes (Kondracki 1989, Coldea 1991, Plašienka et al. 1997). Because of the high geological and geomorphological heterogeneity, crossroad-like geographical position, extent and isolation, the Carpathians are a centre of biodiversity, including many endemic taxa (Mráz & Ronikier 2016). The study area is situated on the transition between oceanic and continental climate (Fig. 1). The sampled plots occur in areas with mean annual temperature between -1 and 10.4 °C (mean 5.4 °C) and annual precipitation between 556 and 1631 mm (mean 963 mm/year). The altitude of study sites varied between ~ 107 m a.s.l. (foothills of the Vihorlat Mts, literature data from Petránová 1967) and 1810 m a.s.l. (the Rodnei Mts). For the distribution of climate data within the study data set, see Electronic Appendix 1.

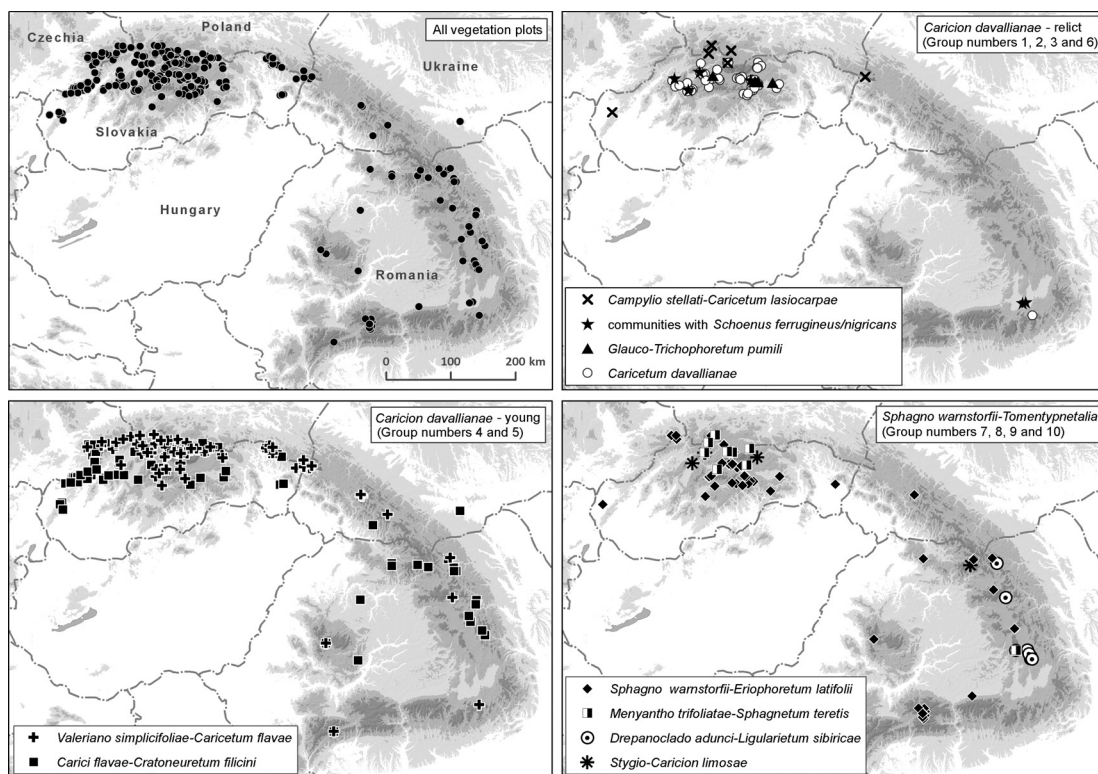


Fig. 1. – Distribution of vegetation-plot records and delimited vegetation units in the Carpathians.

Data sampling and selection

To the analysed data set, we mainly included our original data sampled between 1996 and 2018 by the same sampling protocol, with the same effort to identify bryophytes and the same taxonomic concepts used (altogether 477 records). We focused on rich, extremely rich and calcareous sedge-moss fens as these habitats are characterized in Hájek et al. (2006), i.e. on the *Caricetalia davallianae* and *Sphagno-Tomentypnetalia* orders (Mucina et al. 2016). We sampled the vegetation where calcicole fen species, diagnostic of these orders (Mucina et al. 2016), obviously dominated over other species regarding their richness or cover, and the moss cover composed of non-sphagnaceous fen brown mosses. If *Sphagnum* species were present, we sampled the vegetation where calcium-tolerant species (*S. warnstorffii*, *S. teres*, *S. contortum*) coexist with at least one calcicole species diagnostic of the study vegetation orders. We utilized both literature data and our searching to discover the target vegetation in the field. In the Western Carpathians, the target vegetation has been frequently discovered in the field by the conspicuous growths of cotton sedges visible from hundreds of meters. Aerial images where the system of spring streams or pools was detectable also helped us to identify potential study sites. The focus on the *Caricetalia davallianae* and *Sphagno-Tomentypnetalia* orders caused that this study covers the alkaline part of the pH/calcium gradient occurring in mires. For the distribution of pH and conductivity data within the study data set, see Electronic Appendix 1.

In the field, we delimited a plot of homogeneous surface and vegetation structure in the middle part of each fen site or each habitat segment if a fen composed of more habitats as defined in Hájek et al. (2006). In these plots we recorded all vascular plants and bryophytes using the nine-grade Braun-Blanquet scale for the estimation of abundance and cover (r = few individuals covering < 1% of the area; + = more individuals covering < 1%; 1 = cover 1–5%; 2m = many tiny individuals or ramets covering < 5%; 2a = cover 5–15%; 2b = cover 15–25%; 3 = cover 25–50%; 4 = cover 50–75%; 5 = cover 75–100%). For numerical analyses, this scale was reduced to three cut levels (see below). The total percentage cover of bryophytes and vascular plants were recorded as well. The standard plot size was 4 × 4 m² size (366 plots, 70.4% of the data set), but in 65 cases of small patches of the target vegetation, a smaller plot was used to keep homogeneity of sampled vegetation (42 plots of 9–15 m²; 7 plots of 1–8 m²). Larger plots of 20–30 m² were occasionally used in the early years of our research in all countries involved (84 plots). Five plots taken from Morariu et al. (1985; see below) were of 100 m² area. Peterka et al. (2020) has demonstrated that these plot sizes may be safely merged in broad-scale analyses of fen vegetation without introducing substantial bias, at least when compared with other possible uncertainty sources. They further found that species-area curves of specialists increased negligibly in this plot size range, advocating analyses of the number of specialized fen species. We used all our unpublished, original data from the Eastern and Southern Carpathians and Apuseni Mts in the classification process. For the Western Carpathians, we filtered data by keeping only vegetation-plot records for which we measured pH and conductivity. This step reduced the number of samples from the Western Carpathians relative to the Eastern Carpathians and balanced the data set.

We initially tried to put together as most data as possible, including literature data. In this paper, we finally used only our data, with few exceptions mentioned below. The reason for this decision is that whenever we included literature data (e.g. Soó 1944, 1949, Grodzińska 1961, 1975, Kornaś & Medwecka-Kornaś 1967, Petránová 1967, Coldea 1990, Felbaba-Klushyna 2010), any unsupervised or semi-supervised classification tended to cluster vegetation-plot records by individual authors. For Polish papers, this phenomenon is demonstrated in Hájek (1999). Individual authors obviously used different sampling effort in searching for low-abundant vascular plants (the number of species in a vegetation-plot record differs substantially among the authors), different preciseness in the identification of bryophytes, different taxonomic resolution in important aggregates (e.g. *Carex flava* agg.), different plot sizes, and different strategy of plot selection of sampling; many of them focused on a single or two dominant species in order to reproduce vegetation associations listed in national or regional vegetation surveys. These characteristics of published data sets bias unsupervised and semi-supervised classifications, over-rate regional variation over ecological one and prevent rigorous testing of compositional differentiation at a large scale that involves more countries. We made an exception from using only our data for the original type material of the most problematic associations whose distribution has been so far restricted by state borders. We included original material of *Valeriano simplicifoliae-Caricetum flavae* (Pawlovski et al. 1960; 32 records), along with vegetation-plot records from Petránová (1967), the single report on *Carici flavae-Eriophoretum latifolii* in the Western Carpathians (three records after random selection of one plot per locality), and Morariu et al. (1985), the most important report of *Caricetum davallianae* Dutoit 1924 in Romania with identified bryophytes and

with the species that characterize this unit (five records). Finally, we worked with 517 records. After all classification procedures were finalized, we further aimed to assign the obviously incomplete vegetation-plot records from the original material of *Carici flavae-Eriophoretum* (Soó 1944, 1949) to the final phytosociological units established using the frequency-positive fidelity index (Tichý 2005), the normalized weirdness method (van Tongeren et al. 2008) and supervised k-means. The same procedure has been done with the nomenclature type of *Carici flavae-Blysmetum compressi* from Coldea (1973). These methods are usually used to assign complete vegetation-plot records to the existing vegetation types and differ by whether and how they consider species with high fidelity to clusters. Because we do not know which species were not recorded by Soó (1944, 1949), we used all these methods to obtain a more robust estimation of which vegetation types were actually sampled in these historical records.

Environmental variables

To characterize the vegetation types ecologically, we use a range of environmental variables. They were either measured directly in the field, or estimated using indicator values, or extracted from thematic maps (pH and electric conductivity of groundwater, ecological indicator values for water level, elevation, annual precipitation, mean annual temperature and number of hot days with maximum temperature above 30 °C). In most vegetation-plot records, we measured near-surface groundwater pH and conductivity directly in the field using portable devices, usually in the middle of the vegetation plot in the wettest spots. Water conductivity was used as a reliable proxy of calcium richness. Hájek et al. (2021) report the regression coefficient $R^2 = 0.84$ between conductivity and calcium concentration in groundwater at the European scale.

Some of our older vegetation-plot records from the Eastern Carpathians (Ukraine, Poland and Romania, years 1995–2002) and literature lacked measured pH and conductivity. We imputed them using the MOSS+ method of Tichý et al. (2010), using arithmetic means of the five most similar vegetation-plot records (employing the Bray-Curtis distance).

The geographical coordinates have been either measured directly in the field by GPS device or derived from maps in the case of old vegetation-plot records before 2003 with an accuracy of dozens or few hundreds of meters. Based on geographic coordinates, climatic variables (annual precipitation, mean annual temperature and number of hot days above 30 °C) from 1961 to 2010 was obtained for each site using the CARPATCLIM database (Antolović et al. 2013; www.carpatclim-eu.org). To characterize the water regime, we calculated the means of updated hydrological indicator values for vascular plants and bryophytes in mires weighted by ecological tolerances (Hájek et al. 2020a). The traditional Ellenberg-type ecological indicator values (EIV) were used, but means calculated by the minimum value of the tolerance range (called ‘drought intolerance’ in Hájek et al. 2020a) highly correlated with them ($r = 0.95$, $P < 0.001$). These hydrological indicator values (Hájek et al. 2020a) correlate more strongly with water level than soil moisture (Hájek et al. 2020a). We, therefore, refer to this variable as ‘water level’.

Nomenclature

The nomenclature was harmonized following Euro+Med (2006–2021) for vascular plants and Kučera et al. (2012) for bryophytes. Critical taxa, not always reliably differentiated in the field and literary sources, were merged to aggregates: *Alchemilla vulgaris* agg. (all *Alchemilla* species), *Anthoxanthum odoratum* agg. (*A. alpinum*, *A. odoratum*), *Scorpidium revolvens* agg. (mostly *S. cossonii*, in few cases *S. revolvens*), *Molinia caerulea* agg. (*M. arundinacea* subsp. *arundinacea*, *M. arundinacea* subsp. *freyi*, *M. caerulea*), *Palustriella commutata* agg. (*P. commutata*, *P. falcata*), *Plagiomnium affine* agg. (*P. affine*, *P. elatum*, *P. ellipticum*), *Sphagnum palustre* agg. (*S. centrale*, *S. palustre*). The list of base-rich fen species was adopted from Horsáková et al. (2018).

Classification of vegetation

We did not aim to reproduce the existing classification systems, either the Western Carpathian or Romanian ones, purely, but aimed to test first whether the existing systems mirror the natural variation in rich and calcareous fens. We, therefore, started with the unsupervised hierarchical classifications. We selected two different approaches, one divisive based on partitioning the principal compositional gradient (modified TWINSpan, Roleček et al. 2009; with total inertia as a measure of cluster heterogeneity), and one based on agglomerative clustering. The beta-flexible clustering method (Lance & Williams 1967) and the Bray-Curtis distance were used for agglomerative clustering. We used $\beta = -0.25$ because, with this value, the classification tends to produce a set of clusters of similar size (Legendre & Legendre 2012). We expected the divisive method would stress the compositional differences along the pH/calcium gradient, which is the dominant gradient in fens along which major vegetation types and habitats are frequently distinguished (Malmer 1986, Hájek et al. 2006, Dítě et al. 2007, Peterka et al. 2017). The agglomerative method was expected to capture ecological or biogeographical exceptionalities that may lead to distinctive species composition. The latter case may hold for Romania, where some vegetation types are reported, unlike other Carpathian countries, such as boreo-continental N-limited fens of *Saxifraga hirculi-Tomentypnion nitentis* alliance (Peterka et al. 2017). The pseudospecies cut levels of 0, 5 and 25% were used in both cluster analyses to take estimated percentage covers of individual species into account. The number of interpreted clusters followed the advice of the OPTIMCLASS 1 algorithm (Tichý et al. 2010), with Fisher exact test threshold for diagnostic species being set to $P < 10^{-5}$. At this P-level, the OPTIMCLASS 1 curve that describes the relationship between the number of clusters and the total number of diagnostic species occurrences starts to flatten when the P-criterion is gradually tightening up by steps of 10^{-1} . Using this setting, we interpret the classification at the final level of 14 clusters for Twinspan and 11 clusters for the beta-flexible clustering method (a turning point of the curve). The resulting clusters and dendrograms of both analyses were interpreted for habitat ecology and existing vegetation classification systems using the diagnostic species of individual clusters. The results of unsupervised classification are summarized in Electronic Appendix 2–3.

Because we aim to revise and unify the phytosociological system for the entire Carpathian territory, we cannot rely only on fully unsupervised classification methods. Agglomerative clustering does not allow individual vegetation observations to be assigned to vegetation types because its hierarchy strongly depends on the structure of the

data set (De Cáceres & Wiser 2012). A similar problem may occur in divisive clustering, where gradient structure strongly affects the results and makes them hardly transferrable to other regions (Bruehlheide & Chytrý 2000). Although we may find support for some vegetation types by interpreting clusters based on diagnostic species, we cannot conclude that other vegetation types do not occur in the study region. Moreover, the distribution of individual vegetation types across the study area may be called into question if only unsupervised classification methods are used because an occurrence of a vegetation type in some country may be based on a random assignment of a record to a cluster that may not be reproduced if the data set will slightly change. For a robust phytosociological conclusion, we need to complement unsupervised methods by the semi-supervised or supervised ones that define membership rules for individual vegetation types (De Cáceres & Wiser 2012) and identify unrecognized vegetation types in the context of the well-defined ones (Tichý et al. 2014). The semi-supervised k-means classification (MacQueen 1967, De Cáceres et al. 2009, Tichý et al. 2014) is a suitable and frequently used semi-supervised method in phytosociology to make a regionally transferrable classification system. The cores of the vegetation types supported by the unsupervised classifications acted as the prototypes in the k-means classification. The k-means algorithm iterates two steps: (i) the assignment of observations to clusters whose prototype is closest in the multivariate attribute space, and (ii) the recalculation of prototype locations. We defined these prototypes using formal logic (Table 1). We created the COCKTAIL species groups (Bruehlheide & Chytrý 2000) and formal definitions to identify prototypes of each vegetation type based on combination of species groups (Electronic Appendix 4, Table 2). According to these formal definitions, we could classify 335 vegetation-plot records, i.e. 64.5% of the data set, into 10 prototypes (Table 2). The other records were classified by the k-means algorithm, allowing the appearance of new clusters. As in unsupervised methods, three pseudospecies cut levels were used to consider species covers (0, 5, 25%). We played around the different settings of classification, with a different number of random seeds starting the algorithm (up to 30), a different number of vegetation-plot records to define the centroid, and the different resulting number of clusters (up to 16) in order to obtain robust arguments about the number of eventual additional vegetation types. If a new cluster comprising vegetation-plot records from more than one site has appeared, we checked it for diagnostic species and syntaxonomical or ecological interpretation.

To create a final synoptic table, to obtain the final list of diagnostic species and map the distribution of individual vegetation types, we performed the supervised k-means clustering with the number of clusters corresponding to the number of syntaxonomically interpretable vegetation types appearing in the previous steps. We consider the species diagnostic if it shows both the non-standardized phi-coefficient to a respective cluster (Tichý 2005) higher than 0.25 and simultaneously the statistically significant association with the cluster ($P < 0.001$; Fisher exact test). In the synoptic table, we present the diagnostic species, species occurring in at least 100 vegetation-plot records and other base-rich fen species.

All classification analyses were done using an open interface between the JUICE, PC-ORD 5 (Grandin 2006) and R (<http://www.sci.muni.cz/botany/juice>), the package vegan, version 2.2-0. (Oksanen et al. 2014).

Table 1. – Review of the syntaxonomical units at the association and alliance levels reported from the study area (the Western, Eastern and Southern Carpathian Mts) compiled from Dítě et al. (2007), Hájek & Háberová (2001), Coldea (1977, 1997), Coldea et al. (2008), Hájek (1999), Pawłowski et al. (1960), Peterka et al. (2017), Felbaba-Klushyna (2010) and Chytrý et al. (2020). The right column indicates vegetation types reproduced by unsupervised classifications, and therefore we created the formal definition of their cores to define prototypes for semi-supervised k-means clustering. ¹ The *Caricion atrofusco-saxatilis* vegetation, reported by Coldea et al. (2008) and Chytrý et al. (2020), was not included in the numerical analyses because of a lack of records in which bryophytes were identified.

Vegetation unit	Country	Core defined
<i>Caricion davallianae</i> Klika 1934	CZ, SK, PL, UA, RO	
<i>Campylio-Caricetum lasiocarpae</i> Klötzli 1969	SK	Yes
<i>Caricetum davallianae</i> Dutoit 1924	SK, UA, RO	Yes
<i>Carici-Blysmetum compressi</i> Eggler 1933	UA, RO	No
<i>Carici flavae-Cratoneuretum filicini</i> Kovács et Felföldy 1960	CZ, SK	Yes
<i>Carici flavae-Eriophoretum latifolii</i> Soó 1944	SK, UA, RO	No
<i>Eleocharitetum pauciflorae</i> Lüdi 1921	CZ, SK	No
<i>Glauco-Trichophoretum pumili</i> Vicherek 1973	SK	Yes
<i>Orchido-Schoenetum nigricantis</i> Oberdorfer 1957 + <i>Schoenetum ferruginei</i> Du Rietz 1925	SK, RO	Yes
<i>Seslerietum uliginosae</i> Palmgren 1916	SK, RO	No
<i>Valeriano simplicifoliae-Caricetum flavae</i> Pawłowski et al. 1960	CZ, SK, PL, UA, RO	Yes
<i>Caricion atrofusco-saxatilis</i> Nordhagen 1943	RO	No ¹
<i>Sphagno warnstorffii-Tomentypnion</i> Dahl 1956	CZ, SK, PL, UA, RO	
<i>Menyantho-Sphagnetum teretis</i> Warén 1926	SK	Yes
<i>Sphagno warnstorffii-Caricetum davallianae</i> Rybníček 1984	SK	No
<i>Sphagno warnstorffii-Eriophoretum latifolii</i> Rybníček 1974	CZ, SK, PL	Yes
<i>Stygio-Caricion limosae</i> Nordhagen 1936	SK, RO	Yes
<i>Amblystegio scorpioidis-Caricetum limosae</i> Osvald 1923	SK	No
<i>Swertion perennis-Caricetum chordorhizae</i> Coldea (1986) 1990	RO	No
<i>Saxifrago hirculi-Tomentypnion nitentis</i> Lapshina 2010	RO	Yes

Principal coordinate analysis

To reveal compositional variation in our dataset, we subjected a species-by-site matrix to principal coordinate analysis (PCoA), an unconstrained ordination technique, with the Bray-Curtis dissimilarity distance. We transformed the abundance of individual species to the three pseudospecies cut levels (0, 5 and 25%) and down-weighted rare species. The analysis and its visualization were conducted using an open interface between the JUICE and R (<http://www.sci.muni.cz/botany/juice/>), the package vegan, version 2.2-0. (Oksanen et al. 2014). We calculated the Spearman's rank correlation coefficient between the site scores on the main two ordination axes and measured pH and conductivity, estimated water level, and the number of species of base-rich fens.

Differences among vegetation types

Differences among vegetation types in edaphic and climatic variables were visualized by box-and-whisker plots showing medians, interquartile ranges, extremes and outliers, and tested by Kruskal-Wallis non-parametric test, followed by non-parametric Mann-Whitney pairwise test with Bonferroni correction (other variables). All analyses were done using the Past 4 software (Hammer et al. 2001).

Table 2. – Formal definition of cores of associations and alliances acting as prototypes in k-means clustering and their distribution. Core refers to the distribution based on formal definitions (prototypes used in k-means clustering). Satellite refers to the distribution of a respective cluster after the run of k-means clustering. Explanation of formal logic: <###species name> refers to species group (Electronic Appendix 4), <species name GR05> refers to cover above a given threshold (%).

Association	Formal definition
<i>Caricion davallianae</i>	
1. <i>Caricetum davallianae</i> Core+satellite: SK, PL + RO	<###Primula farinosa>NOT((((<Sphagnum spp. GR00>OR<###Triglochin maritima>)OR<Schoenus ferrugineus GR05>)OR<###Palustriella commutata>)OR<Palustriella commutata GR05>)
2. <i>Glauco-Trichophoretum pumili</i> Core: SK	<###Triglochin maritima>NOT(<Schoenus nigricans GR05>OR<Schoenus ferrugineus GR05>)
3. <i>Orchido-Schoenetum nigricantis</i> Core: RO + <i>Schoenus ferrugineus</i> fens; Core: SK	<Schoenus nigricans GR05>OR<Schoenus ferrugineus GR05>
4. <i>Carici flavae-Cratoneuretum filicini</i> Core+satellite: CZ, SK, PL, RO + UA	(<###Palustriella commutata>OR<Palustriella commutata GR05>)NOT((((<###Primula farinosa2>OR<###Triglochin maritima>)OR(<Schoenus nigricans GR05>OR<Schoenus ferrugineus GR05>))OR<###Valeriana dioica subsp. simplicifolia>)
5. <i>Valeriano simplicifolia-Caricetum flavae</i> Core+satellite: CZ, SK, PL, RO + UA	(<###Valeriana dioica subsp. simplicifolia>AND<###Eriophorum latifolium>)NOT((((<Sphagnum spp. GR00>OR<###Palustriella commutata>)OR<###Primula farinosa>)OR<Schoenus nigricans GR05>)OR<Schoenus ferrugineus GR05>)OR<Carex lasiocarpa GR05>)
6. <i>Campylio-Caricetum lasiocarpae</i> Core: SK, PL	(<###Eriophorum latifolium>AND(<Carex lasiocarpa GR05>OR<Carex diandra GR05>))NOT(<Sphagnum spp. GR05>OR<#TCScorpidium scorpioides GR00>)
7. <i>Stygio-Caricion limosae</i> Core: SK, RO	(<###Carex limosa>AND(<#TCScorpidium scorpioides GR05>OR<###Scorpidium scorpioides>))NOT<Sphagnum spp. GR05>
<i>Saxifrago hirculi-Tomentypnion nitentis</i>	
8. <i>Drepanoclado adunci-Ligularietum sibiricae</i> ass. nova; Core: RO	<###Ligularia sibirica>NOT<Sphagnum spp. GR05>
<i>Sphagno warnstorffii-Tomentypnion nitentis</i>	
9. <i>Menyantho-Sphagnetum teretis</i> Core: SK, PL, RO	(((((<Carex chordorrhiza GR05>OR<Carex lasiocarpa GR05>)OR<Carex limosa GR05>)OR<Carex diandra GR05>)OR<###Scorpidium scorpioides>)AND<Sphagnum spp. GR05>
10. <i>Sphagno warnstorffii-Eriophoretum latifolii</i> Core+satellite: CZ, SK, PL, RO + UA	(<###Eriophorum latifolium>AND(<###Sphagnum warnstorffii>OR<Sphagnum warnstorffii GR05>))NOT((((<###Primula farinosa>OR<Carex chordorrhiza GR05>)OR<Carex lasiocarpa GR05>)OR<Carex limosa GR05>)OR<Carex diandra GR05>)OR<###Scorpidium scorpioides>)

Results

Unsupervised hierarchical clustering

At the highest level of the modified Twinspan (Electronic Appendix 2), three major groups of vegetation-plot records may be identified, according to their diagnostic species, as (i) the rich and extremely rich fens (*Sphagno-Tomentypnetalia* fens, according to Mucina et al. 2016), (ii) calcareous fens with the indicators of relict fens (Hájek et al. 2011), (iii) younger calcareous fen grasslands of the *Carici flavae-Cratoneuretum filicini*

and *Valeriano simplicifoliae-Caricetum flavae* association that mutually differentiated at the level of seven clusters. At the level of 14 clusters, most of the previously recognized vegetation types appeared.

The beta-flexible clustering method yielded similar results, but because of its agglomerative nature, it better delimited rare vegetation types forming small clusters not defined by principal gradients, such as the *Schoenus*-dominated fens, the *Stygio-Caricion limosae* cluster of calcareous quaking fens, defined by boreo-continental relict species and specific hydrology (Peterka et al. 2018), the two small groups characterized by high-mountain species and the group of tall-sedge fens (Electronic Appendix 3). When the number of clusters increased to 13, one cluster split into three clusters, out of which two clusters corresponded to rare vegetation types previously recognized in the Carpathians: the *Saxifraga hirculi-Tomentypnion* alliance, defined by the nature of nutrient limitation (Peterka et al. 2017), and the *Campylio-Caricetum lasiocarpae* association defined by a combination of hydrology, base saturation and specific regional history. Contrary to the Twinspan classification, the highest level of the Beta Flexible classification did not perfectly separate phytosociological orders or relict fens from younger ones. The character species suggest the prominent role of nutrient availability and calcium richness (Electronic Appendix 3).

Semi-supervised and supervised classification

The runs of semi-supervised k-means (with 10 prototypes defined at the basis of unsupervised classifications) with a low number of starts did not recognise any new vegetation type that would comprise vegetation-plot records from more than one site. It essentially created new clusters consisting of one record. If we had increased the number of starts, one or two more numerous groups of vegetation-plot records rich in accidental grassland species appeared, but they lacked diagnostic species except for some generalist grassland species. Their ecological or syntaxonomical interpretation was unclear because they grouped vegetation-plot records from strongly tufa-forming fens, strongly peat-forming fens and mineral soils together and lacked a geographical pattern (results not shown). The original classification of individual vegetation-plot records within these additional clusters corresponded to the associations from other, previously delimited clusters (*Carici flavae-Cratoneuretum filicini* and *Valeriano-Caricetum flavae*). We, therefore, decided to set the final number of clusters to ten, corresponding to the number of prototypes (i.e. we run supervised classification). The final classification yielded a sufficient number of diagnostic species for each cluster, including mire specialists (Table 3). Out of 10 vegetation types, the one had to be formally described as the new association (the *Drepanoclado aduncii-Ligularietum sibiricae*). The principal reason is that no association of the *Saxifraga hirculi-Tomentypnion nitentis* alliance (compare Peterka et al. 2017) has been formally described in or even reported from Europe so far. Four associations (*Carici flavae-Cratoneuretum filicini*, *Valeriano-Caricetum flavae*, *Menyantho-Sphagnetum teretis*, *Sphagno warnstorii-Eriophoretum latifolii*) are newly reported for Romania. Three associations are new for Ukraine (the same, except for *Valeriano-Caricetum flavae*), and two associations are new for Polish Carpathians (*Carici flavae-Cratoneuretum filicini*, *Menyantho-Sphagnetum teretis*). Our synthesis found no support for distinguishing four associations reported in national and regional vegetation surveys: *Carici-Blysmetum compressi*,

Table 3. – Synoptic table with species frequencies in 10 finally delimited phytosociological units (k-means clustering). Diagnostic species are sorted according to the phi-coefficient. Species with the phi-coefficient above 0.25 are highlighted by slight grey, species with the phi-coefficient higher than 0.35 are highlighted by dark grey colour. Other species occurring in at least 100 vegetation-plot records and other species of base-rich fens are included.

Cluster	1	2	3	4	5	6	7	8	9	10
Number of vegetation-plot records	79	9	10	120	136	12	10	12	22	109
Mean number of species	32.3	19.2	27.3	37.8	10.9	27.6	19.5	42.6	35.6	41.0
1. <i>Caricetum davallianae</i>										
<i>Primula farinosa</i>	82	67	90	4	2	0	10	8	0	17
<i>Carex davalliana</i>	100	0	50	22	37	0	0	0	23	34
<i>Carex hostiana</i>	39	0	40	3	1	8	0	8	0	5
<i>Carex lepidocarpa</i>	51	0	60	21	7	8	20	42	5	13
<i>Sesleria uliginosa</i>	16	0	20	0	0	0	0	0	0	0
<i>Pinguicula vulgaris</i>	69	22	90	4	43	33	50	0	18	27
<i>Salix repens</i> subsp. <i>rosmarinifolia</i>	23	0	20	4	1	0	0	42	0	6
<i>Scorpidium revolvens</i> agg.	92	0	50	28	79	58	100	8	59	44
2. <i>Glauco-Trichophoretum pumili</i>										
<i>Plantago maritima</i>	0	89	0	0	0	0	0	0	0	0
<i>Trichophorum pumilum</i>	1	89	10	0	0	0	0	0	0	0
<i>Glaux maritima</i>	0	67	0	0	0	0	0	0	0	0
<i>Campyliadelphus elodes</i>	0	44	0	0	0	0	0	0	0	0
<i>Centaurium uliginosum</i>	0	44	10	0	0	0	0	0	0	0
<i>Triglochin maritima</i>	14	100	40	1	4	0	0	25	0	1
<i>Odontites vulgaris</i>	0	33	0	1	1	0	0	0	0	0
<i>Carex distans</i>	3	89	20	18	1	0	0	0	0	3
<i>Schoenoplectus tabernaemontani</i>	3	89	40	0	1	0	0	8	0	1
3. <i>Junco subnodulosi</i>-<i>Schoenetum nigricantis</i> and <i>Schoenus ferrugineus</i> fens										
<i>Schoenus ferrugineus</i>	1	0	80	0	0	0	0	0	0	0
<i>Schoenus nigricans</i>	0	0	20	0	0	0	0	0	0	0
<i>Equisetum ramosissimum</i>	0	0	20	0	0	0	0	0	0	0
<i>Allium flavum</i>	0	0	20	0	0	0	0	0	0	0
<i>Molinia caerulea</i> agg.	42	33	100	13	9	33	20	33	23	29
4. <i>Carici flavae</i>-<i>Cratoneuretum filicini</i>										
<i>Juncus inflexus</i>	5	0	10	48	3	0	0	0	0	0
<i>Eupatorium cannabinum</i>	13	0	50	57	9	0	0	8	0	2
<i>Palustriella commutata</i> agg.	40	0	60	83	30	8	30	8	0	9
<i>Tussilago farfara</i>	8	0	10	41	9	0	0	0	0	1
<i>Carex flacca</i>	40	0	20	58	8	0	0	0	5	7
<i>Mentha longifolia</i>	8	0	0	35	4	8	0	0	0	2
<i>Hypericum tetrapterum</i>	0	0	0	23	2	8	0	0	0	1
<i>Agrostis stolonifera</i>	12	33	10	53	27	0	0	25	5	18
<i>Ranunculus repens</i>	0	0	0	22	4	0	0	0	0	3
<i>Equisetum arvense</i>	16	11	0	49	25	0	0	8	0	17
<i>Lythrum salicaria</i>	4	0	10	36	9	17	0	42	5	11
<i>Lysimachia nummularia</i>	1	0	0	18	2	0	0	8	0	2
<i>Ajuga reptans</i>	4	0	0	25	12	0	0	0	0	1
<i>Carex hirta</i>	1	11	0	12	0	0	0	0	0	0
<i>Potentilla reptans</i>	0	0	0	9	0	0	0	0	0	0
<i>Carex tomentosa</i>	0	0	0	9	0	0	0	0	0	0
<i>Scirpus sylvaticus</i>	4	0	0	29	14	0	0	8	0	10

Cluster	1	2	3	4	5	6	7	8	9	10
Number of vegetation-plot records	79	9	10	120	136	12	10	12	22	109
Mean number of species	32.3	19.2	27.3	37.8	10.9	27.6	19.5	42.6	35.6	41.0

5. *Valeriano simplicifoliae*-*Caricetum flavae*

<i>Valeriana dioica</i> subsp. <i>simplicifolia</i>	51	0	10	35	83	58	0	0	64	46
<i>Linum catharticum</i>	13	0	20	39	63	0	0	25	18	21
<i>Alchemilla vulgaris</i> agg.	1	0	0	18	46	0	0	0	5	20
<i>Prunella vulgaris</i>	10	0	10	38	64	0	0	8	5	35
<i>Leontodon hispidus</i>	4	0	20	17	43	0	0	0	27	16
<i>Crepis paludosa</i>	43	0	0	33	78	67	0	42	68	52
<i>Trifolium pratense</i>	5	22	0	8	32	0	0	0	0	11
<i>Rhinanthus minor</i>	1	0	0	3	21	0	0	8	0	5
<i>Briza media</i>	39	22	20	60	84	17	0	58	68	54
<i>Rhinanthus alectorolophus</i> agg.	0	0	0	0	11	0	0	0	0	0
<i>Dactylorhiza majalis</i>	45	11	10	53	79	58	20	25	59	51
<i>Ranunculus acris</i>	23	44	0	56	66	17	0	25	18	34
<i>Plagiomnium affine</i> agg.	69	0	20	63	84	42	20	67	32	49
<i>Equisetum variegatum</i>	13	11	20	3	25	8	0	0	0	5
<i>Caltha palustris</i>	13	0	10	41	54	0	0	25	5	31

6. *Campylio stellati-Caricetum lasiocarpae*

<i>Typha latifolia</i>	0	0	0	0	0	17	0	0	0	0
<i>Hamatocaulis vernicosus</i>	0	0	0	0	6	58	0	33	23	24
<i>Carex lasiocarpa</i>	0	0	0	0	1	100	0	8	36	0
<i>Menyanthes trifoliata</i>	19	0	0	4	13	83	70	42	64	15

7. *Amblystegio scorpioidis*-*Caricetum limosae* and *Swertio perennis*-*Caricetum chordorrhizae*

<i>Drepanocladus trifarius</i>	1	0	0	0	0	0	50	0	18	0
<i>Oncophorus virens</i>	0	0	0	0	0	0	20	0	0	0
<i>Ligusticum mutellina</i>	0	0	0	2	0	0	30	0	0	0
<i>Scorpidium scorpioides</i>	0	0	0	0	0	0	40	0	18	0
<i>Carex limosa</i>	6	0	0	0	0	8	70	8	36	2
<i>Carex chordorrhiza</i>	0	0	0	1	0	25	60	0	32	3
<i>Carex demissa</i>	0	0	0	1	2	0	40	0	9	6

8. *Drepanoclado adunci-Ligularietum sibiricae*

<i>Drepanocladus aduncus</i>	1	0	0	2	2	0	0	67	5	1
<i>Ligularia sibirica</i>	3	0	10	0	0	0	0	67	5	6
<i>Marchantia polymorpha</i>	4	0	0	3	5	0	10	58	5	5
<i>Geranium palustre</i>	3	0	0	1	1	0	0	33	0	2
<i>Carex diandra</i>	5	0	10	2	4	0	0	50	14	2

9. *Menyantho trifoliatae-Sphagnetum teretis*

<i>Vaccinium oxycoccos</i>	0	0	0	0	1	25	30	0	86	17
<i>Drosera anglica</i>	5	0	0	0	0	0	30	8	27	2
<i>Persicaria officinalis</i>	3	0	0	0	8	8	0	0	36	6
<i>Sphagnum fallax</i>	1	0	0	0	1	0	0	0	27	9

10. *Sphagno warnstorffii*-*Eriophoretum latifolii*

<i>Drosera rotundifolia</i>	1	0	0	0	1	0	10	8	36	45
<i>Straminergon stramineum</i>	0	0	0	0	0	0	0	0	23	37
<i>Aulacomnium palustre</i>	17	0	0	3	29	33	0	58	77	75
<i>Sphagnum contortum</i>	0	0	0	0	2	0	30	0	45	36
<i>Sarmentypnum exannulatum</i>	1	0	0	0	0	0	0	0	9	24
<i>Carex echinata</i>	0	0	0	30	40	8	10	25	36	68
<i>Nardus stricta</i>	0	0	0	3	8	0	10	0	0	28
<i>Sphagnum palustre</i> agg.	0	0	0	0	0	0	0	0	9	17

Cluster	1	2	3	4	5	6	7	8	9	10
Number of vegetation-plot records	79	9	10	120	136	12	10	12	22	109
Mean number of species	32.3	19.2	27.3	37.8	10.9	27.6	19.5	42.6	35.6	41.0
<i>Sphagnum subsecundum</i>	0	0	0	0	1	0	0	0	0	16
<i>Paludella squarrosa</i>	0	0	0	0	0	0	0	0	14	15
<i>Sphagnum angustifolium</i>	0	0	0	0	0	0	0	8	14	16
<i>Luzula sudetica</i>	0	0	0	1	2	0	10	0	0	16
<i>Agrostis canina</i>	4	0	0	12	20	8	0	33	41	41
<i>Viola palustris</i>	0	0	0	0	9	8	20	8	18	24
<i>Atrichum undulatum</i>	0	0	0	0	2	0	0	0	0	12
<i>Epilobium palustre</i>	4	0	10	13	21	8	0	58	18	40
<i>Vaccinium vitis-idaea</i>	1	0	0	0	0	0	0	0	0	9
<i>Galium uliginosum</i>	19	0	10	8	33	75	0	92	50	54
<i>Eriophorum vaginatum</i>	0	0	0	2	0	0	0	0	0	10
<i>Sphagnum teres</i>	1	0	0	0	1	0	10	0	68	47
<i>Sphagnum warnstorffii</i>	3	0	0	0	2	0	0	0	77	72
<i>Sphagnum subnitens</i>	0	0	0	0	0	0	0	0	41	25
<i>Sphagnum flexuosum</i>	0	0	0	0	1	0	0	8	36	19
Other species										
<i>Potentilla erecta</i>	97	11	100	80	94	92	20	67	91	96
<i>Bryum pseudotriquetrum</i>	83	33	70	83	93	75	60	100	59	72
<i>Carex panicea</i>	90	11	50	79	93	83	50	50	82	71
<i>Campylium stellatum</i>	90	56	90	68	82	83	60	75	77	70
<i>Eriophorum latifolium</i>	83	11	50	83	88	42	30	42	55	61
<i>Calliergonella cuspidata</i>	58	0	60	85	73	67	0	92	50	67
<i>Eriophorum angustifolium</i>	78	0	40	62	64	75	50	42	77	66
<i>Equisetum palustre</i>	78	0	30	64	80	92	10	67	64	38
<i>Carex nigra</i> agg.	47	11	20	44	76	42	60	83	64	78
<i>Juncus articulatus</i>	60	56	70	77	68	33	0	67	36	45
<i>Parnassia palustris</i>	77	89	100	34	57	17	40	92	9	50
<i>Carex flava</i>	13	0	0	61	67	42	60	17	64	60
<i>Festuca rubra</i> agg.	31	44	0	53	50	25	0	75	59	66
<i>Cirsium palustre</i>	32	0	40	38	46	58	0	8	45	51
<i>Triglochin palustris</i>	62	89	30	49	38	33	30	0	14	28
<i>Cirsium rivulare</i>	35	0	30	61	54	17	0	17	5	19
<i>Epipactis palustris</i>	40	22	70	46	43	42	10	83	32	18
<i>Tomentypnum nitens</i>	34	0	10	12	41	50	0	83	55	59
<i>Fissidens adianthoides</i>	49	0	20	38	37	33	0	17	27	32
<i>Carex rostrata</i>	49	0	0	9	23	58	90	100	73	50
<i>Succisa pratensis</i>	49	11	70	35	15	50	0	58	23	43
<i>Aneura pinguis</i>	25	11	60	35	19	33	40	83	45	45
<i>Climacium dendroides</i>	12	0	10	28	45	0	0	33	18	44
<i>Equisetum fluviatile</i>	13	0	0	17	46	33	20	83	50	34
<i>Carex dioica</i>	35	0	0	1	42	33	0	42	59	43
<i>Eleocharis quinqueflora</i>	51	11	40	11	27	67	70	33	32	18
<i>Philonotis calcarea</i>	25	0	10	40	34	17	10	17	5	9
<i>Filipendula ulmaria</i>	19	0	0	13	24	8	0	58	27	45
<i>Galium palustre</i>	6	0	0	19	26	17	0	33	27	39
<i>Anthoxanthum odoratum</i> agg.	3	0	0	18	38	8	0	17	5	35
<i>Lathyrus pratensis</i>	19	0	0	21	36	8	0	0	5	21
<i>Angelica sylvestris</i>	17	0	0	21	14	50	0	25	41	28
<i>Blysmus compressus</i>	23	67	20	23	21	0	0	50	5	9
<i>Geum rivale</i>	4	0	0	12	36	0	0	8	23	27
<i>Juncus alpinoarticulatus</i>	9	0	0	5	11	8	10	33	0	7
<i>Swertia perennis</i>	6	0	10	5	4	0	30	17	0	3
<i>Dactylorhiza incarnata</i>	12	11	10	10	1	0	10	42	5	2

Eleocharitetum pauciflorae, *Carici flavae-Eriophoretum* and *Sphagno warnstorffii-Caricetum davallianae* (see Discussion for detailed reasoning). Calcareous fens with the presence of *Sesleria uliginosa* were classified as *Caricetum davallianae*, in line with the previous study of Gonda & Dítě (2011).

Identified alliances

The distinguished vegetation types belong to the four alliances accepted in the pan-European concept of Mucina et al. (2016). One of them belongs to the calcareous fens of *Caricetalia davallianae* order (the *Caricion davallianae* alliance), and three of them belong to boreo-continental rich and extremely-rich fens of the *Sphagno warnstorffii-Tomentypnietalia nitentis* order (the *Stygio-Caricion limosae*, *Saxifrago hirculi-Tomentypnion nitentis* and *Sphagno warnstorffii-Tomentypnion nitentis* alliances) (Electronic Appendix 5).

The highest pH characterizes *Caricion davallianae* out of all alliances (Fig. 2). The lowest values of water pH and conductivity were found for *Sphagno warnstorffii-Tomentypnion nitentis* and *Stygio-Caricion limosae*. The *Stygio-Caricion limosae* alliance showed the highest water level (Fig. 2) that support the presence of relic bryophytes *Scorpidium scorpioides* and *Calliergon trifarium* and relic fen sedges *Carex limosa* and *Carex chordorrhiza*.

In terms of climate, *Saxifrago hirculi-Tomentypnion nitentis* occurs in the driest, i.e. the most continental, areas with the lowest precipitation sum. In contrast, *Sphagno warnstorffii-Tomentypnion nitentis* occurs in regions with the highest annual precipitation, lowest annual temperature and lowest number of hot days.

Identified associations: *Caricetalia davallianae* order

There are six associations defined within *Caricion davallianae* alliance (Electronic Appendix 5) that mutually differ in edaphic and climate variables (Fig. 4, Table 4). The association *Caricetum davallianae* has a distribution centre in the Western Carpathians (Slovakia), with only a few records from Eastern Carpathians (Romania, Braşov district, data from Morariu et al. 1985). It is rich in species (on average, 32 species per vegetation-plot record) and simultaneously rich in species specialized to base-rich fens. Some of them (*Carex davalliana*, *C. hostiana*, *C. lepidocarpa*, *Primula farinosa*, *Sesleria uliginosa* and *Pinguicula vulgaris*) act as diagnostic species. The association occupies fens of high pH and conductivity and high water level in regions with annual precipitation sum around 900 mm, mean annual temperature around 6 °C and the low number of hot days (Fig. 3).

The *Glauco-Trichophoretum pumili* association is restricted only to travertine fens of the Western Carpathians with specific warm continental climate supporting both the travertine formation and the occurrence of relict species of a continental distribution range. Travertine fens are saturated by groundwater of a deep circulation, extremely rich in minerals. It leads to the highest water conductivity among all vegetation types. The diagnostic species (*Plantago maritima*, *Trichophorum pumilum*, *Glaux maritima*, *Triglochin maritima*) tolerate high concentrations of salts. Due to extreme conditions leading to a low number of generalist species, this vegetation type is the poorest in species.

Communities with *Schoenus* species, belonging probably to two different associations (Tables 1, 2), are characterized by the high cover of either *S. ferrugineus* (Slovakia) or *S. nigricans* (Romania). They are relatively species-poor (27 species on average) and rare

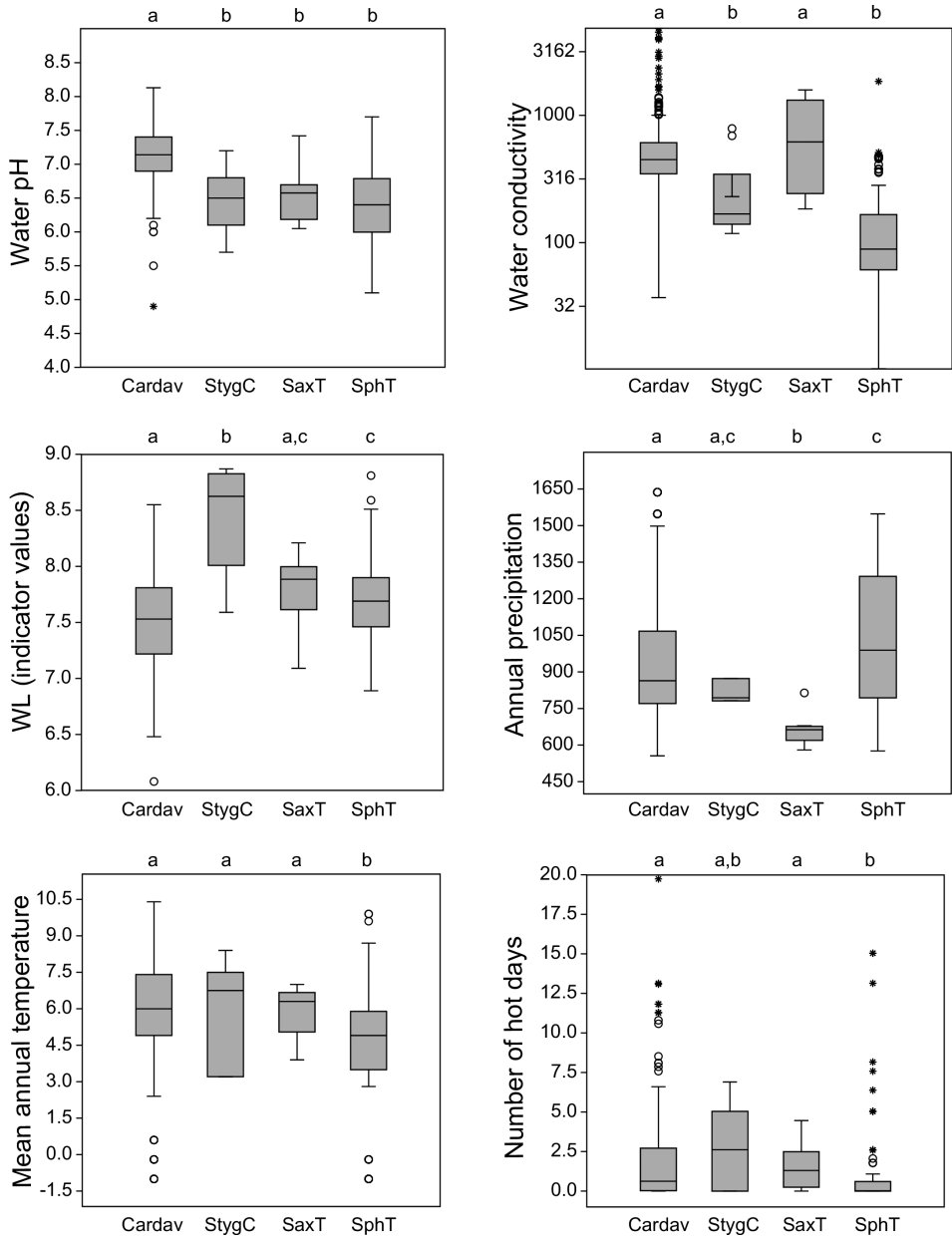


Fig. 2. – Box-and-whisker plots showing medians, interquartile ranges, extremes and outliers of edaphic and climatic variables for individual alliances. The different letters above boxplots indicate significant differences among alliances (*Caricion davallianae*, *Stygio-Caricion limosae*, *Saxifraga hirculi-Tomentypnion nitentis*, *Sphagno warnstorffii-Tomentypnion nitentis*).

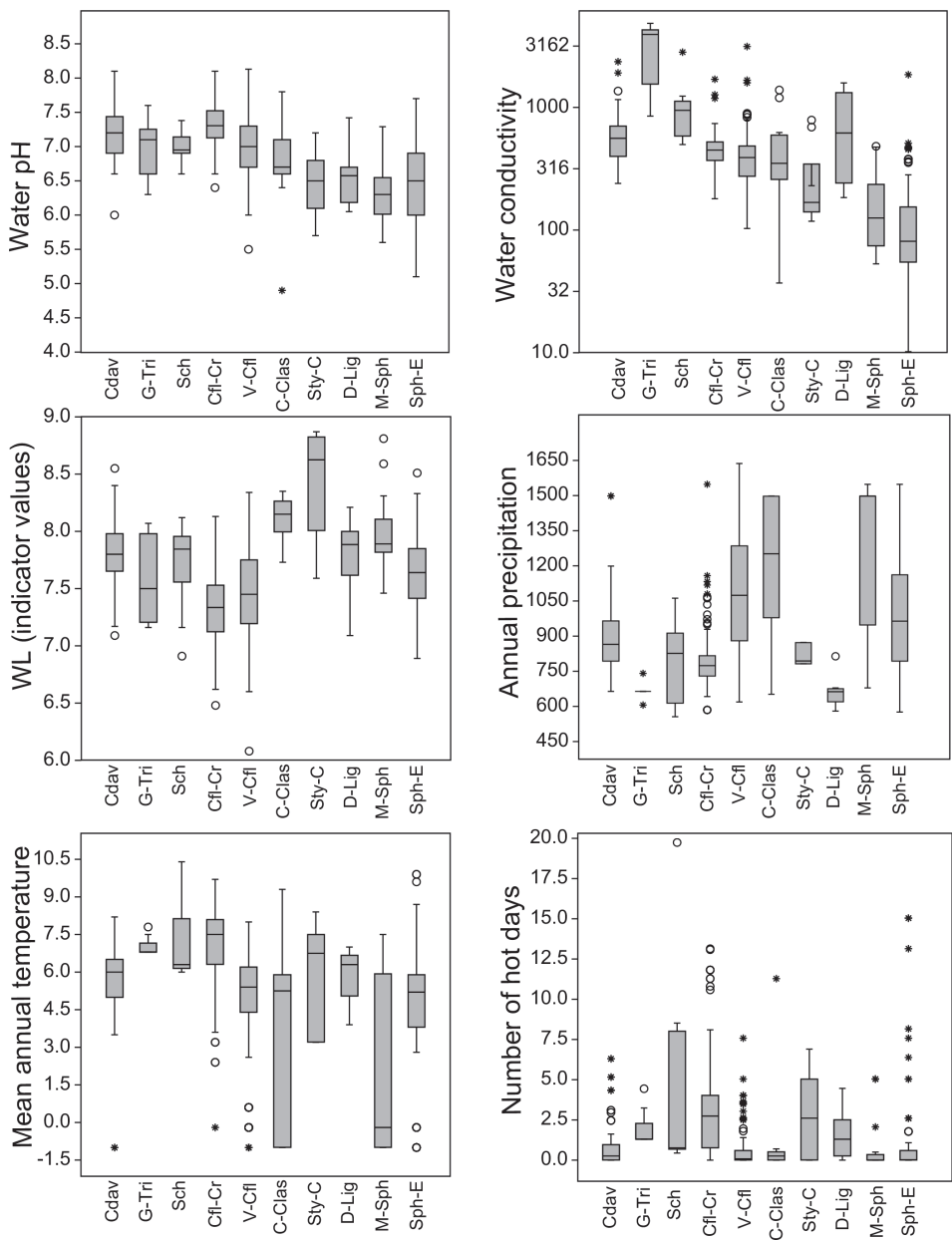


Fig. 3. – Box-and-whisker plots showing medians, interquartile ranges, extremes and outliers of edaphic and climatic variables for 10 vegetation types delimited in our study. See Table 4 for the statistical significance of differences. Abbreviations of vegetation types: Cdav – *Caricetum davallianae* ass., G-Tri – *Glauco-Trichophoretum pumili* ass., Sch – *Orchido-Schoenetum nigricantis* ass. + *Schoenus ferrugineus* fens, Cfl-Cr – *Carici flavae-Cratoneuretum filicini* ass., V-Cfl – *Valeriano simplicifolia-Caricetum flavae* ass., C-Clas – *Campyllo-Caricetum lasiocarpae* ass., Sty-C – *Stygio-Caricion limosae* all., Dre-L – *Drepanoclado adunci-Ligularietum sibiricae* ass., M-Sph – *Menyantho-Sphagnetum teretis* ass., Sp-E – *Sphagno warnstorffii-Eriophoretum latifolii* ass.

Vegetation types	EUNIS 2020	Habitat Directive
<i>Glauco-Trichophoretum pumili</i>	Q46 Carpathian travertine fens	7220 * Petrifying springs with tufa formation
<i>Carici flavae-Cratoneuretum</i>	Q41 Alkaline, calcareous, carbonate-rich small-sedge spring fens	
<i>Caricetum davallianae</i>		7230 Alkaline fens
<i>Valeriano simplicifoliae-Caricetum flavae</i>		
<i>Schoenus ferrugineus</i> fens		
<i>Orchido-Schoenetum nigricantis</i>	Q43 Tall-sedge base-rich fens	
<i>Campylio-Caricetum lasiocarpae</i>		
<i>Drepanoclado adunci-Ligularietum sibiricae</i>	Q42 Extremely rich moss-sedge fens	
<i>Sphagno warnstorffii-Eriophoretum latifolii</i>		
<i>Menyantho-Sphagnetum teretis</i>	Q44 Calcareous quaking mire	
<i>Amblystegio-Caricetum limosae</i>		
<i>Swertio-Caricetum chordorrhizae</i>	Q45 Arctic-alpine rich fens	
<i>Caricion atrofusco-saxatilis*</i>		
		7240 * Alpine pioneer formations of <i>Caricion bicoloris-atrofuscae</i>

* see comment below Table 1

* see comment below Table 1

Fig. 4. – The conversion of delimited vegetation types into EUNIS (Chytrý et al. 2020) and Habitat Directive classification schemes.

in their distribution. Their habitat conditions are characterized by high water conductivity, decreased water level and occurrence under drier and warmer conditions than most other vegetation types.

The *Carici flavae-Cratoneuretum filicini* association is widely distributed throughout the entire Carpathian range. It is differentiated from other units by *Juncus inflexus*, *Eupatorium cannabinum*, *Palustriella commutata* agg., *Tussilago farfara*, *Carex flacca* and *Mentha longifolia* and characterized by the highest water pH, high water conductivity and surface calcium-carbonate (tufa) precipitation. It occurs in areas with significantly lower precipitation and higher mean annual temperature and the number of hot days, unlike the other association of younger fen grasslands, the *Valeriano simplicifoliae-Caricetum flavae*.

Apart from the occurrence in colder mountain areas, the *Valeriano simplicifoliae-Caricetum flavae* association further differs from the previous association by somewhat lower water pH and conductivity values and lack of tufa precipitation. This difference determines its different assignment in the Habitat Directive scheme (Fig. 4). The diagnostic species include *Valeriana dioica* subsp. *simplicifolia*, *Linum catharticum*, *Alchemilla vulgaris* agg., and some wet-meadow species that co-occur with diagnostic species of the *Caricetalia davallianae* order.

The *Campylio-Caricetum lasiocarpae* association is rare in the Carpathians, occurring only in the Western Carpathians (Slovakia, Poland). The association is compositionally transitional to the *Sphagno warnstorffii-Tomentypnetalia nitentis* order because of fen sedges with a boreal distribution range. It shows the highest water levels within the

Table 4. – Differences in edaphic and climatic variables among the delimited vegetation types, indicated by the significance levels of the Mann-Whitney pairwise test with Bonferroni correction. The bold font refers to the differences at the $P < 0.001$ level, while the standard font refers to the $P < 0.01$ level. The Kruskal-Wallis nonparametric test was significant for all variables at the $P < 0.001$ level. 1 – *Caricetum davallianae*, 2 – *Glauco-Trichophoretum pumili*, 3 – *Orchido-Schoenetum nigricantis* + *Schoenus ferrugineus* fens, 4 – *Carici flavae-Cratoneuretum filicini*, 5 – *Valeriano simplicifoliae-Caricetum flavae*, 6 – *Campylio stellati-Caricetum lasiocarpae*, 7 – *Stygio – Caricion limosae*, 8 – *Drepanoclado adunci-Ligularietum sibiricae*, 9 – *Menyantho-Sphagnetum teretis*, 10 – *Sphagno warnstorffii-Eriophoretum latifolii*. pH – water reaction, cond. – water conductivity (in $\mu\text{S}\cdot\text{cm}^{-1}$), WL – water level (ecological indicator value), temp – mean annual temperature (1961–2010), prec – annual precipitation (in mm; 1961–2010), hot days – number of hot days (above 30 °C) per year (1961–2010), fen spec – number of fen specialists.

1.	2.	3.	4.	5	6	7.	8.	9.	10.
1. X	cond, prec, fen spec	–	WL, temp, prec, hot days, fen spec	cond, WL, temp, prec, fen spec	fen spec, WL	pH, cond, WL, fen spec	pH, prec, fen spec	pH, cond, WL, temp, prec, fen spec	pH, cond, temp, fen spec
2.	X	fen spec	cond, prec	cond, temp, prec, hot days, fen spec	cond, WL, temp, prec	cond, prec	cond	cond, WL, temp, prec	cond, temp, prec
3.		X	cond, fen spec	cond, temp, prec, hot days	Temp, WL	WL, fen spec	–	pH, cond, WL, temp, prec, fen spec	cond, temp, fen spec
4.			X	pH, WL, temp, prec, hot days, fen spec	pH, WL, temp, prec, hot days	pH, WL	pH, WL, prec	pH, cond, WL, temp, prec, hot days	pH, cond, WL, temp, prec, hot days
5.				X	WL	pH, WL, prec, fen spec	pH, WL, prec	pH, cond, WL, fen spec	pH, cond, WL, prec, fen spec
6.					X	prec	prec	–	cond, WL
7.						X	prec	–	WL
8.							X	cond, prec	cond, prec
9.								X	WL
10.									x

Caricetalia davallianae order, nearly as high as found for the *Stygio-Caricion limosae* alliance. The occurrence of *Carex lasiocarpa*, *Hamatocaulis vernicosus* and *Menyanthes trifoliata*, which all occur here with the highest frequency among all *Caricion davallianae* associations, is shared with the *Sphagno warnstorffii-Tomentypnetalia nitentis* order as well. The association occurs in quite wet and cold areas.

Identified associations: Sphagno warnstorffii-Tomentypnetalia nitentis order

The *Stygio-Caricion limosae* alliance of boreo-continental quaking fens comprises two associations in the Carpathians, but they could not be well delimited in our study because of their rarity. In Slovakia, the alliance occurs only in two fens, represented by the *Amblystegio scorpioidis-Caricetum limosae* Osvald 1923 association. In Romania, the

alliance occurs only in the Rodnei Mts, represented by the *Swertio perennis*-*Caricetum chordorrhizae* Coldea (1986)1990 association.

We delimited two associations within the *Sphagno warnstorffii*-*Tomentypnion nitentis* alliance: *Menyantho-Sphagnetum teretis* (Slovakia, Poland, one record in Romania) and *Sphagno warnstorffii*-*Eriophoretum latifolii* (all countries). *Menyanthes trifoliata*, fen sedges of boreal distribution (*C. limosa*, *C. chordorrhiza*, *C. lasiocarpa*), *Vaccinium oxycoccus* and *Drosera anglica*, differentiated the former. Contrary to the latter, it occurs under higher conductivity, water level and annual precipitation, and lower annual temperature. The *Sphagno warnstorffii*-*Eriophoretum latifolii* is characterized by *Drosera rotundifolia*, *Straminergon stramineum*, *Aulacomnium palustre*, *Sphagnum contortum* and *Sarmentypnum exannulatum*.

The alliance *Saxifraga hirculi*-*Tomentypnion nitentis* occurs only in the Eastern Carpathians in Romania. Because there is no association of this alliance described in Europe so far, we had to describe the new association *Drepanoclado adunci*-*Ligularietum sibiricae*, whose diagnostic species involve *Ligularia sibirica*, *Drepanocladus aduncus*, *Marchantia polymorpha* and *Carex diandra*. This association is species-rich, with an average number of 43 species per vegetation-plot record, the highest value among all clusters. The *Drepanoclado adunci*-*Ligularietum sibiricae* occurs under drier and warmer conditions as compared to other vegetation types of the order.

Nomenclatural type of *Drepanoclado adunci*-*Ligularietum sibiricae*, ass. nova

Romania, Harghita Mts, Vlăhița pass, the Dumbrava fen, Longitude: 25°35'59.7", Latitude: 46°19'03.3", Turboveg no. 487833, Field number 9/2014, Date: 6 August 2014, Relevé area: 16 m², Altitude: 805, a. s. l., Slope (degrees): 0, Cover herb layer: 70 %, Cover moss layer: 98 %, pH: 6.7, Conductivity of groundwater 741 μS·cm⁻¹, Authors: Petra Hájková, Daniel Dítě, Irina Goia, Michal Hájek.

E₁: *Ligularia sibirica* 2a, *Saxifraga hirculus* 2a, *Epipactis palustris* 2a, *Carex rostrata* 2a, *Parnassia palustris* 1, *Drosera rotundifolia* 1, *Galium uliginosum* 1, *Lysimachia vulgaris* 1, *Carex nigra* 1, *Equisetum fluviatile* 1, *Succisa pratensis* 1, *Equisetum palustre* 1, *Thelypteris palustris* 1, *Valeriana dioica* 1, *Carex dioica* +, *Eriophorum angustifolium* +, *Festuca rubra* +, *Cardamine pratensis* +, *Lychnis flos-cuculi* +, *Myosotis nemorosa* +, *Crepis paludosa* +, *Poa trivialis* +, *Rumex acetosa* +, *Epilobium palustre* +, *Dactylorhiza maculata* r.

E₀: *Tomentypnum nitens* 3, *Aulacomnium palustre* 2b, *Marchantia polymorpha* 2a, *Calliergonella cuspidata* 2a, *Bryum pseudotriquetrum* 1, *Plagiomnium ellipticum* +, *Drepanocladus aduncus* +, *Sphagnum angustifolium* +, *Aneura pinguis* +.

The main compositional variation

The first PCoA (Fig. 5) axis stretches from relict fens (*Caricetum davallianae*, *Schoenus*-dominated fens, travertine fens of *Glauco-Trichophoretum pumili*, calcareous quaking fens of *Stygio-Caricion limosae*) to younger fen grasslands (*Carici flavae*-*Cratoneuretum filicini*, *Valeriano simplicifoliae*-*Caricetum flavae*, *Sphagno warnstorffii*-*Eriophoretum latifolii*). This gradient is well characterized by the decreasing number of species of base-rich fens and partially also by pH and conductivity because the most alkaline and calcium-rich vegetation types (*Schoenus*-dominated fens and travertine fens of *Glauco-Trichophoretum pumili*) are relict ones. In contrast, the least calcareous fens (*Sphagno warnstorffii*-*Eriophoretum latifolii*) are located right on the first axis. Water level contributes to the formation of this compositional gradient as well, being higher in relict fens.

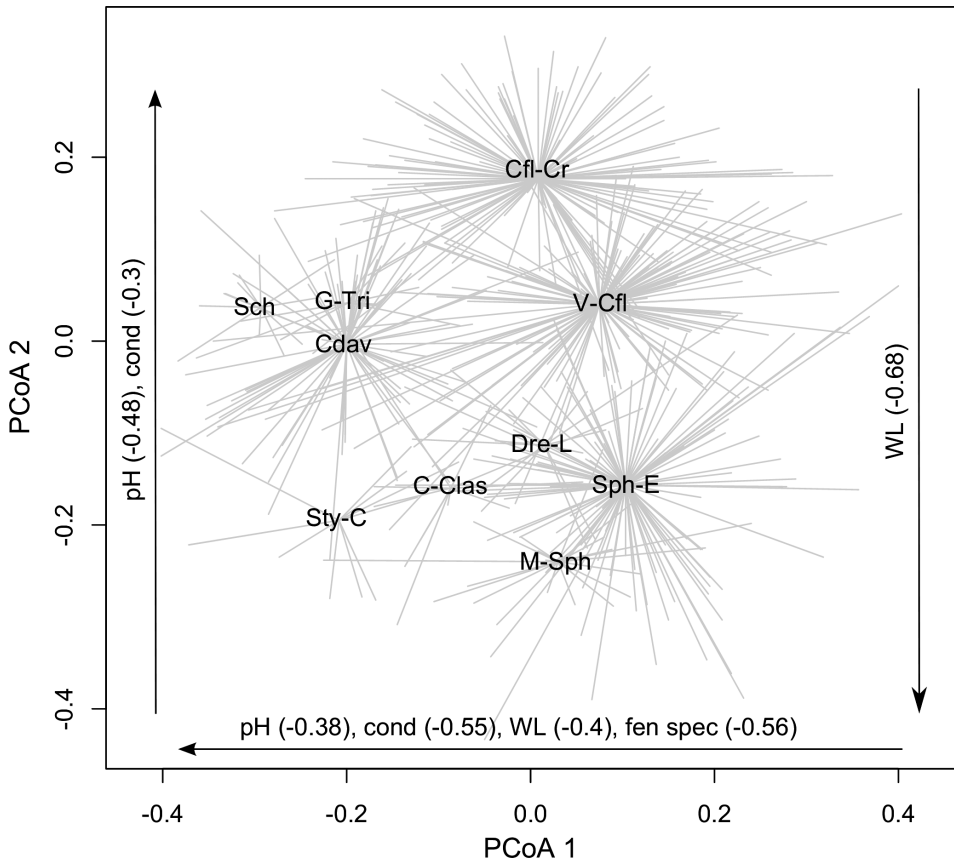


Fig. 5. – PCoA ordination scatters, with spider plots and centroids of 10 delimited vegetation units. The Spearman's rank correlation coefficients between the two principal PCoA axes and tested variables, significant at the adjusted $P < 0.001$ (Bonferonni correction), are shown. Abbreviations of vegetation types: Cdav – *Caricetum davallianae* ass., G-Tri – *Glauco-Trichophoretum pumili* ass., Sch – *Orchido-Schoenetum nigricantis* ass. + *Schoenus ferrugineus* fens, Cfl-Cr – *Carici flavae-Cratoneuretum filicini* ass., V-Cfl – *Valeriano simplicifolia-Caricetum flavae* ass., C-Clas – *Campylio-Caricetum lasiocarpae* ass., Sty-C – *Stygio-Caricion limosae* all., Dre-L – *Drepanoclado adunci-Ligularietum sibiricae* ass., M-Sph – *Menyantho-Sphagnetum teretis* ass., Sp-E – *Sphagno warnstorffii-Eriophoretum latifolii* ass. Abbreviations of tested factors: WL – water level, cond – electrical conductivity of groundwater, fen spec – the number of base-rich fen species.

The second PCoA axis stretches from tufa-forming younger fen grasslands (*Carici flavae-Cratoneuretum filicini*) to relict vegetation types characterized by boreal sedges and boreal brown mosses (*Stygio-Caricion limosae*, *Campylio-Caricetum lasiocarpae*, *Menyantho-Sphagnetum teretis*). This gradient strongly coincides with the water level and less clearly with pH and conductivity being lower in the vegetation types with boreal sedges and brown mosses.

Discussion

Major ecological factors and their relevance for vegetation classification

Calcium richness and differences between relict, usually well-waterlogged fens and younger fen grasslands, govern vegetation variability of the Carpathian fens. We did not find a support for the geographical differentiation of younger fen grasslands into the one Eastern-Carpathian and the two Western-Carpathian associations, as suggested by current national vegetation monographs. Therefore, the broad-scale geographical gradients connected to biogeography, macroclimate or cultural differences in fen usage seem to be of minor importance.

The first divisions in the classification separate the rich and extremely rich fens of the *Sphagno-Tomentypnetalia* order, occurring in all Carpathian countries, from calcareous fens of the *Caricetalia davallianae* order, mirroring the classification scheme of European fens as presented in the EuroVeg checklist (Mucina et al. 2016). This result supports distinguishing rich fens with calcium-tolerant peatmosses into the separate alliance *Sphagno warnstorffii-Tomentypnion nitentis*. These rich fens strongly differ from calcareous fens of the *Caricion davallianae* also by assemblages of invertebrates (Horsák & Hájek 2003, Opravilová & Hájek 2006, Bojková et al. 2011, Zhai et al. 2015) and belong to different habitats than calcareous fens in the EUNIS system (Chytrý et al. 2020) and Habitat Directive (Evans 2006). This alliance, and its associations, had been distinguished only in Slovakia (Hájek & Háberová 2001, Dítě et al. 2007), Czech Republic (Rybníček et al. 1984, Hájek & Hájková 2011) and only locally in Poland (Hájek & Hájková 2002). It had not been distinguished at all in Romania and Ukraine, where it was primarily classified within the *Carici flavae-Eriophoretum* association because of the occurrence of the name-giving species and due to the lack of broad-scale comparisons. Another alliance from the *Sphagno-Tomentypnetalia* order that appeared to be new for Romania, the *Saxifrago hirculi-Tomentypnion nitentis*, had been distinguished in Europe relatively recently (Peterka et al. 2017). Its specific combination of species, quite similar across Eurasia, is determined by a high phosphorus concentration relative to nitrogen concentration, resulting in a low N-to-P ratio in vegetation (Pawlikovski et al. 2013, Peterka et al. 2017). Both the high concentration of iron and the continental climate slow down the succession that would otherwise go fast in P-enriched sites (Hájek et al. 2020b). These conditions are met in the Harghita region in Romania, where the core of this vegetation is located. Because this vegetation had not been recognized previously as a separate entity, we had to describe a new association (the *Drepanoclado adunci-Ligularietum sibiricae*). The name-giving moss *Drepanocladus aduncus* is a wetland moss species with great P-demands that occur in alluvial grasslands and nutrient-rich reed beds and ponds rather than in true fens (Dierßen 2001, Hedenäs 2003). It also occurs in the original diagnosis of the alliance from Western Siberia (Lapshina 2010). The name-giving vascular plant, *Ligularia sibirica*, is relict species in the Carpathians, associated with a boreo-continental climate (Dítě et al. 2018), and shapes the physiognomy of the association substantially in the Eastern Carpathians. Last, in line with the previous studies of Peterka et al. (2017, 2018), we report the *Stygio-Caricion limosae* alliance in Romania. A single association *Swertio-Caricetum chordorrhizae* Coldea (1986) 1990 belongs to this alliance in Romania. In the Romanian national vegetation survey (Coldea 1997), this vegetation had been assigned to the *Caricion lasiocarpae* alliance that is no longer accepted at the European level (Mucina et al. 2016, Peterka et al. 2017).

The other significant factors that shape vegetation variability in Carpathian fens are associated with habitat history, water level and the nature of nutrient limitation. The habitat history, stressed especially by the Twinspan classification at the level of three clusters and by the first PCoA axis, differentiates relict calcareous fens from fen grasslands of more recent origin. The calcareous fen grasslands belong to the *Carici flavae-Cratoneuretum filicini* and *Valeriano simplicifoliae-Caricetum flavae* associations, while rich-fen grasslands with *Sphagnum* mosses belong to the *Sphagno warnstorffii-Eriophoretum latifolii* association; the position of these three associations differ along the second PCoA axis. The vegetation of these younger fen grasslands has initiated in the late Holocene onwards, often as late as during medieval or postmedieval colonizations. In the significant parts of the Outer Carpathians, they represent the only calcareous and rich-fen vegetation (Horsák et al. 2007, Hájková et al. 2012). In other vegetation types, species considered glacial or early-Holocene relicts (Dítě et al. 2018) are much more represented. They are mainly concentrated in the semi-aquatic habitats of *Stygio-Caricion limosae* alliance and terrestrial habitats of managed travertine fens (the *Glauco-Trichophoretum pumili* association (Dítě et al. 2013, Hájková et al. 2020). This pattern suggests that different environmental conditions (high water level, travertine precipitation, anthropogenic disturbances in the forested phases of the Holocene) facilitate habitat persistence in different sites (Hájek et al. 2020b, Hájková et al. 2020).

The effects of relictualism and habitat history on the species composition of calcareous fens had been previously identified by Morariu et al. (1985) and Horsák et al. (2007), the latter also using land snails. Some species that characterize relict vegetation types, such as *Primula farinosa*, appeared to show a statistically significant affinity to relict fens initiating before the Middle Holocene in the study of Hájek et al. (2011). These historical effects seem to apply not only to plants and snails but also to some groups of aquatic invertebrates (Horsák et al. 2015). They had been reflected in the Czech and Slovak national vegetation surveys (Dítě et al. 2007, Hájek & Hájková 2011) at the association level, unlike Romania, Ukraine and Poland where the dominance of a single species (*C. davalliana*) was a priority criterion (Coldea 1997, Felbaba-Klushyna 2010). We have identified that these relict vegetation types of the most calcareous fens have their distribution centre in the Inner Western Carpathians where the relict fens have been indeed frequently reported (Hájková et al. 2012, 2015, 2020); in other countries, they have been recorded only rarely (Romania: Morariu et al. 1985). Outside the Western Carpathians, they are abundant in the Alps (e.g. Moravec 1966, Gerdol et al. 1994, Conradi & Friedmann 2013).

Young calcareous fens had been consistently classified into the tufa-forming fens (called *Carici flavae-Cratoneuretum filicini* in the Czech Republic, Hungary and Slovakia, Kovács & Felföldy 1960, Dítě et al. 2007, Hájek & Hájková 2011) and peat-forming, more mountain fens (called *Valeriano simplicifoliae-Caricetum flavae* in Poland, Czech Republic and Slovakia; Pawłowski et al. 1960, Dítě et al. 2007, Hájek & Hájková 2011). These vegetation types occur across the Carpathians, including Eastern and Southern Carpathians (Ukraine, Romania). Semi-supervised classification had not disrupted this result and did not suggest any new vegetation type that would occur only in the Eastern Carpathians, as suggested by the previously declared distribution of the *Carici flavae-Eriophoretum*. By analogy, none of either unsupervised or supervised classifications has brought any support for distinguishing the vegetation types based on the dominance of

Blysmus compressus or *Eleocharis quinqueflora*, respectively. These species occurred and sometimes even dominated (with Braun-Blanquet cover code equal to or higher than 2) in virtually all vegetation types distinguished by our methods.

The nature of nutrient limitation and nutrient availability, being associated with the occurrence of grassland, tall-sedge and reed-bed species with high phosphorus and potassium demands (Rozbrojová & Hájek 2008, Pawlikovski et al. 2013, Hájek et al. 2014) contributes to the delimitation of the *Saxifraga hirculi-Tomentypnion nitentis* alliance from the *Caricetalia davallianae* fens (Pawlikovski et al. 2013, Peterka et al. 2017) and the delimitation of *Valeriano simplicifoliae-Caricetum flavae* association from the *Carici flavae-Cratoneuretum filicini* association. In the latter association, tufa formation causes phosphorus binding to carbonates (Boyer & Wheeler 1989, Rozbrojová & Hájek 2008) and hence weak colonization of fens by nutrient-demanding grassland species from the surroundings (Hettenbergerová & Hájek 2011).

Nomenclatural teasers

The delimited vegetation types are well transferrable to individual national vegetation surveys, especially those that recognized tufa-forming from peat-forming fens. However, the problems may appear if the association names should match the Code of Phytosociological Nomenclature (Theurillat et al. 2020). The names *Carici flavae-Eriophoretum* Soó 1944 and *Carici-Blysmetum compressi* Eggler 1933 have been used, especially in Romania, for the vegetation that belongs to several different associations (Electronic Appendix 6), as demonstrated by our study. However, these names are validly described according to the Code and are older than the names *Valeriano simplicifoliae-Caricetum flavae* and *Carici flavae-Cratoneuretum filicini*. The correct way should be to identify these names with one of the currently recognized associations and use them instead of later described names. For *Carici flavae-Eriophoretum*, this procedure is quite complicated because original vegetation-plot records published in Soó (1944) are species-poor, making their assignment to the recognized vegetation types difficult. According to the FFPI index (Tichý et al. 2010), the material is close to the *Valeriano simplicifoliae-Caricetum flavae* association (Electronic Appendix 6). The type vegetation-plot record (the only vegetation-plot record containing both name-giving taxa; Theurillat et al. 2020) is closest to this association, but it had been sampled in the limestone area where we recorded only the vegetation of the *Carici flavae-Cratoneuretum filicini* association (the Haşmaş Mts). The reason for such a result may lie in the apparent incompleteness of Soó's vegetation-plot records. Later material of this association published by Soó (1949) and Pop et al. (1960, 1962) is no longer similar to *Valeriano simplicifoliae-Caricetum flavae*, but rather to other vegetation units, frequently to *Carici flavae-Cratoneuretum filicini*. The name *Carici flavae-Eriophoretum* was used for several different associations as recognized in our study. For these reasons, we have kept the nomenclature as in the studies from the Western Carpathians and will prepare a suggestion to the nomenclatural committee to assign the name as *nomen ambiguum* to meet the articles of the Code.

By analogy, we cannot assign the name *Carici-Blysmetum compressi* Eggler 1933 to any of our associations. Its nomenclatural type comes from outside our study area (Styria region in Austria) and is obviously incomplete in species composition. Eggler (1933) amalgamated the unspecified number of graminoid species into the "other graminoids"

group, preventing unequivocal assignment of this unit to some of our associations. Coldea (1997) was aware of this problem and has suggested a new name, *Carici flavae-Blysmetum compressi*, but the way he refers to the previous publications made this name superfluous (*nomen superfluum*, Art. 29c of the Code) and hence illegitimate. According to the nomenclatural type, this name would be an exact younger syntaxonomical synonym of *Valeriano simplicifoliae-Caricetum flavae* association; it even fully matches its formal definition as presented in this paper (Electronic Appendix 7).

The name *Eleocharitetum pauciflorae* Lüdi 1921, which used to be identified with *Eleocharis quinqueflora*-dominated and otherwise species-poor fens, is the oldest validly described name within the study vegetation of calcareous fens. As such, it should be used as a valid name for some association.

Both names, *Carici-Blysmetum compressi* and *Eleocharitetum pauciflorae* can be kept for extremely species-poor monodominant vegetation at specific sites such as initial successional phases of pool or shallow-lake terrestrialization (*Eleocharitetum pauciflorae*) or heavily-grazed wetlands and initial successional phases on abandoned tracks, quarries, river banks, sand pits or landslides (both associations, especially *Carici-Blysmetum compressi*). Such relevés have been only rarely represented in our study, and respective clusters, therefore, could hardly appear. These monodominant vegetation types had been distinguished only in some countries. Critical revision at the European scale is therefore needed.

A conversion of phytosociological associations into EUNIS and Habitat Directive habitats

Regardless of which association name will be finally used for tufa-forming fens, the distinguishing of this association (here called *Carici flavae-Cratoneuretum filicini*) will allow easy conversion to habitat “Petrifying fens with tufa formation” (Fig. 4), a priority habitat of Habitat Directive (the Natura 2000 network). This habitat has already been recognized in Romania (Gafta & Mountford 2008, Doniță et al. 2005), and an easy link to phytosociological classification could lead to the more effective selection of individual sites for legal protection. The same habitat directive unit also includes relict travertine fens (*Glaucio-Trichophoretum pumili*) in Slovakia, which have recently been accepted as a separate EUNIS habitat (Chytrý et al. 2020).

The delimitation of the *Stygio-Caricion limosae* alliance in the Carpathians will allow a more direct link between the Eunis habitat “calcareous quaking fens” (Chytrý et al. 2020) and the phytosociological system (Peterka et al. 2018). The clear delimitation of the *Sphagno warnstorffii-Tomentypnion* alliance in Romania, Ukraine, and Poland will allow a more straightforward conversion between the Eunis (the “Rich fens” unit) and the phytosociological classification as well. We see the unification of the phytosociological classification system in the Carpathian territory, as presented in our paper, as a highly beneficial step to effectively protect the highly endangered biota of Carpathian calcareous fens.

Outline of further research

Apart from solving the syntaxonomically disputable names, with *Carici-Blysmetum compressi* requiring broader geographical focus, the future research should focus on the associations and alliances we recorded only rarely in the Carpathians. We did not reach

a final classification solution for *Schoenus*-dominated fens which are only marginally represented in our data set. The Western-Carpathian ones are dominated by *Schoenus ferrugineus* and are compositionally similar to *Caricetum davallianae* fens (Dítě et al. 2007) or *Schoenus ferrugineus* fens in southernmost Sweden (du Rietz 1925). Contrary, the Eastern-Carpathian ones are dominated by *Schoenus nigricans* and are more similar to suboceanic-submediterranean *S. nigricans* fens (Allorge 1921, Hájek et al. 2008, Seytre et al. 2015). Despite this pattern, the Beta Flexible classification merged them into a single, well-delimited cluster that kept small even after semi-supervised k-means runs. The final solution on their association names cannot be therefore reached without European synthesis.

The beta-flexible clustering method recognized, yet at a very low level of division, one group of tall-sedge fens with the indicators of mineral-soil, nutrient-rich, often lowland, wetlands (*Mentha aquatica*, *Phragmites australis*, *Thelypteris palustris*, *Liparis loeselii*, *Eleocharis uniglumis*, *Carex acutiformis*). This cluster was quite heterogeneous, preventing syntaxonomical interpretation, but it included the vegetation-plot records from Petránová (1967) assigned originally as, again, *Carici flavae-Eriophoretum* association. Similar vegetation had also been described by Soó (1947), under the same name, from Transsilvania, or Hájek et al. (2008), under the name *Eleochariti uniglumis-Caricetum distantis* from Bulgaria and Redzić et al. (2013), under the name *Eriophoro latifolii-Menyanthes trifoliata*, from Herzegovina. It is possible that such lowland fens with tall-sedges, yet without boreo-continental relict species, might represent a specific warmth-tolerating association that reaches the Carpathians only marginally at their warm margins. A wide-scale synthesis covering entire southeastern Europe is needed to resolve this task.

Conclusion

To conclude, the compositional variation in Carpathian calcium-rich fens largely follows the historical factors, differentiating relict fens from young fen grasslands, and local habitat conditions such as precipitation of carbonate tufa, water level or nature of nutrient limitation. There is no support to delimit different vegetation types of widespread young fen grasslands in Western (*Valeriano simplicifoliae-Caricetum flavae*) and Eastern (*Carici flavae-Eriophoretum latifolii*) Carpathians. Instead, distinguishing between peat-forming (*Valeriano simplicifoliae-Caricetum flavae*) and tufa-forming (*Carici flavae-Cratoneuretum filicini*) fen grasslands makes ecological sense, with both types occurring in the entire Carpathians. Regional differences are more evident in relict fens than in young fen grasslands. They are caused by the rarity of specific combinations of edaphic and climatic factors and regional habitat history. The *Drepanoclado adunci-Ligularietum sibiricae*, formally described as the new association in this paper, illustrates this pattern. It belongs to the *Saxifrago hirculi-Tomentypnion nitentis* alliance that comprises N-limited boreocontinental fens and whose distribution is restricted to the Romanian part of the Eastern Carpathians.

See www.preslia.cz for Electronic Appendices 1–7.

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Souhrn

V tomto článku představujeme jednotný klasifikační systém vápnných slatinišť Karpat. Protože fytocenologická klasifikace se dosud výrazně lišila mezi jednotlivými zeměmi, zejména mezi Západními a Východními Karpaty, a rozšíření řady asociací uměle končilo na státní hranici, zapsali jsme velké množství fytocenologických snímků jednotnou metodikou po celém území Karpat. Ve shodě s předchozími ekologickými studiemi ze Západních Karpat odlišovaly neřízené numerické klasifikace jednotlivé vegetační typy podle gradientu nasycení bázemi a podle rozdílu mezi starými, reliktními lokalitami a mladšími slatinnými loukami. Na základě neřízených klasifikací jsme pak formálně definovali jádra deseti vegetačních typů a za pomoci částečně řízené klasifikace (k-means) jsme klasifikovali zbylé snímky a ověřovali, zda datový soubor neukrývá další vegetační typy, neidentifikované předchozími analýzami. Výsledná klasifikace obsahuje deset vegetačních typů, většinou interpretovaných na asociální úrovni. Pět asociací uvádíme jako nové pro Rumunsko. Vegetační typy byly dobře odlišeny analýzou hlavních koordinát, jejíž první dvě osy odrážely nasycení bázemi a rozdíly mezi reliktními a mladšími lokalitami, které souvisely s podílem slatinistních druhů a indikovanou hladinou vody. Klima (teplota, srážky, počet horkých dní) a specifické edafické podmínky se rovněž podílely na diverzifikaci některých vegetačních typů. Naše analýzy podpořily klasifikaci mladších slatinišť na pěnovcové a ukládající slatinu, které patří do různých biotopů Směrnice o stanovištích. Obě takto vymezené asociace se vyskytují ve všech zkoumaných karpatských zemích, včetně Rumunska. Naopak jsme nenašli podporu pro dříve uváděné výhradně východokarpatské asociace. Přinášíme rovněž další silné důkazy pro výskyt řádu *Sphagno warnstorffii-Tomentypnetalia* a jeho svazů *Sphagno warnstorffii-Tomentypnion nitentis*, *Stygio-Caricion limosae* a *Saxifrago hirculi-Tomentypnion* v Rumunsku.

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