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Syntaxonomical revision of the *Triseto flavescentis-Polygonion* bistortae alliance in the Carpathians

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This phytosociological study of the Carpathian species-rich mesophilous mountain hay meadows (Triseto flavescentis-Polygonion bistortae alliance, Molinio-Arrhenatheretea class) presents the first unified large-scale classification system in four countries: Slovakia, Poland, Romania, and Ukraine. The starting dataset contained relevés of the Molinio-Arrhenatheretea, Mulgedio-Aconitetea and Nardetea strictae classes. Numerical classification and semi-supervised classification by K-means method were used for the analyses. An electronic expert system and diagnostic species for grassland vegetation served for identification of a priori groups in K-means method. The final dataset contained 612 relevés. Altitude, climatic data and Ellenberg indicator values were used for ecological differentiation of syntaxa. The main gradients in floristic composition were analysed by Detrended Correspondence Analysis. Finally, the eight well-differentiated associations and one newly described association were determined: Campanulo glomeratae-Geranietum sylvatici, Geranio sylvatici-Trisetetum flavescentis, Crepido mollis-Agrostietum capillaris, Geranio-Alchemilletum crinitae, Alchemillo-Deschampsietum caespitosae, Phyteumo (orbicularis)-Trifolietum pratensis, Astrantio-Trisetetum flavescentis, Trollio altissimi-Knautietum dipsacifoliae and Violo declinatae-Agrostietum capillaris ass. nova. The differences in vegetation diversity of mountain hay meadows between particular countries were confirmed: Alchemillo-Deschampsietum caespitosae occurs in all studied territories, Campanulo glomeratae-Geranietum sylvatici occurs predominantly in Slovakia and the newly described association Violo declinatae-Agrostietum capillaris ass. nova could be found only in Ukraine.

Keywords: Carpathians, diversity, Molinio-Arrhenatheretea, mountain hay meadows, Triseto flavescentis-Polygonion bistortae, semi-supervised classification, syntaxonomical revision

Introduction

The Carpathians are a recognised biodiversity hot-spot, harbouring many relatively undisturbed ecosystems and still rich in semi-natural, traditional landscapes (Björnsen-Gurung et al. 2009; Bálint et al. 2011; Solovyeva et al. 2011; Kliment et al. 2016; Mráz and Ronikier 2016). The species richness and extraordinarily high diversity of Carpathian vegetation is influenced by an important biogeographical position, fragmentation of the mountains, evolution of the vegetation and fauna in the glacial and post-glacial periods, geographical isolation, and a highly diverse geology and relief (Kliment 1999; Webster et al. 2001; Ruffini et al. 2006; Mráz et al. 2007; Björnsen-Gurung et al. 2009; Ronikier 2011; Kadlečík 2016; Kliment et al. 2016; Mráz and Ronikier 2016).

The Carpathian Triseto flavescentis-Polygonion bistortae Br.-Bl. et Tx. exMarschall 1947 alliance includes species-rich mesophilous montane meadows dominated by medium-tall grasses (Agrostis capillaris, Festuca rubra agg., Trisetum flavescens) and broad-leaved herbs (Alchemilla spec. div., Crepis mollis, Geranium sylvaticum, Phyteuma spicatum, Pimpinella major, Astrantia major) on nutrient-rich soils (Chytrý 2007; Hegedüšová and Ružičková 2007; Matuszkiewicz 2008; Hegedüšová et al. 2011a; Korzeniak 2013a; Hegedüšová Vantarová 2014). Although they are spread in the Western Carpathians of Slovakia and Poland, their areas are diminishing and increasingly restricted to the montane-subalpine belt due to both traditional and current land exploitation (Hegedűšová et al. 2011a,b; Korzeniak 2013a; Hegedűšová Vantarová 2014; Pruchniewicz 2017). They occur only in isolated places over calcareous bedrock in the wetter and colder conditions mostly on north-oriented saddles and slopes at 600 to 1700 m a.s.l.; and rarely on non-carbonate substrata (Korzeniak 2013a; Hegedüšová Vantarová 2014). Associations of this alliance have close relationships with Arrhenatherion elatioris, Bromion erecti and Nardo strictae-Agrostion tenuis alliances and it also hosts numerous species from the *Mulgedio-Aconitetea* class. Many endangered, protected and rare species occur here (Ioras 2003; Witkowski 2003; Coldea et al. 2009; Coldea 2012; Korzeniak 2013a; Hegedüšová Vantarová 2014) and some of them have an endemic character (Kliment et al. 2016). These meadows also occur in other temperate European mountain ranges, and become progressively more common in oceanic areas (Chytrý 2007). Their distribution centre is in the Alps (Ellmauer and Mucina 1993; Peter et al. 2008; Pierce et al. 2008). Detailed European distribution is reported by Hegedüšová et al. (2011a). From a nature conservation point of view, mountain hay meadows belong to the NATURA 2000 (6520 - Mountain hay meadows), EUNIS (E2.3 – Mountain hay meadows, E4.5 – Alpine and subalpine enriched grasslands) and CORINE (38.3 Mountain hay meadow).

Syntaxonomical revisions have a proven role in pattern recognition in several scientific fields. An increasing need for reliable and unified vegetation classifications across large regions has resulted in comprehensive supra-national vegetation surveys in several European countries (e.g. Dúbravková et al. 2010; Terzi 2015; Douda et al. 2016; Willner et. al. 2017; Willner et. al. 2019). Also, our study has brought new insights for e syntaxonomical classification of the Triseto-Polygonion alliance on supra-national level. The idea of a common order of mountain hay meadows was firstly adopted by Dierschke (1981) who introduced the syntaxonomy of Triseto-Polygonion alliance in Central Europe. Phytosociological research of these meadows has a long tradition especially in Slovakia (Hadač et al. 1969; Bělohlávková 1980; Ružičková 1997, 2001, 2002b, 2006). Nevertheless, up to the 1980s, only partial data of the vegetation of the *Triseto-Polygonion* alliance were published from particular countries (e.g. Puşcaru et al. 1956; Raclaru 1967; Zanoschi 1971; Sanda et al. 1977; Wojterski 1978). The syntaxonomy of this alliance was published by Sanda et al. (1999) and Coldea (2012) from Romania, Matuszkiewicz (2008) from Poland and Hegedüšová Vantarová (2014) from Slovakia. More detailed national syntaxonomical research was done by Kliment (1994), Ružičková (2002a, 2004), Brinkmann and Reif (2006), Hegedüšová and Ružičková (2007), Hegedüšová et al. (2011a) and Budzhak et al. (2016). Floristic studies were prepared by Mihăilescu (2001) and Coldea (2003). Some information on the studied alliance was published by Malynovskyy et al. (1992) and Solomakha (2008) from Ukraine. Further studies where the management of grasslands of the *Triseto*-Polygonion alliance is mentioned have been published in the last two decades (e.g. Perzanowska et

al. 2004; Brinkmann et al. 2009; Hegedüšová et al. 2011b; Pozynych 2012; Korzeniak 2013a; Vadel and Dražil 2015).

The objectives of our study were (i) to prepare a revised and unified classification system for Carpathian mountain hay meadows of the *Triseto-Polygonion* alliance using formalized supervised and semi-supervised methods, (ii) to resolve some syntaxonomical problems, (iii) to evaluate the ecological variability of the distinguished associations, (iv) to determine the major environmental gradients responsible for variation in the floristic composition and (v) to assess the distribution of the distinguished vegetation units in the Carpathians.

Methods

Study area

The Carpathians are an important biogeographical location between the Balkan ranges in the south, the Alps in the west and the Scandinavian range in the north (Ozenda 1985; Ronikier 2011). They form an arch – the largest European mountain range, spanning Austria (Hainburger Berge), Slovakia, Czech Republic (the Moravian Carpathians, westward up to the Moravian Gate), Hungary (North Hungarian Mountains), Poland, Ukraine, Serbia (amid the river valleys of Morava and Timok, southward up to Niš) and Romania (Kondracki 1978, 1989; Ruffini et al 2006; Ronikier 2011; Hlásny et al. 2016; Kliment et al. 2016). Following the traditional division (Kliment 1999; Mráz 2005; Kliment et al. 2016), the Carpathians are divided into the Western Carpathians (Austria, Czech Republic, Hungary, Slovakia and Poland), Eastern Carpathians (Poland, Slovakia, Ukraine and Romania), Southern Carpathians (Romania and Serbia), Apuseni Mountains (Romania) and the Transylvanian Basin (Romania). They cover total surface of 209,000 km². From a geological viewpoint, the north-western Bulgarian highlands can also be assigned to the Carpathians (cf. Cankov 1974; Kliment et al. 2016) but their boundaries, and especially the inner zonation, have not vet been precisely defined (cf. Pax 1898; Soó 1930, 1933a, b; Balázs 1939; Pawłowski 1969, 1970; Starmühler 1995; Starmühler and Mitka 2001; Ruffini et al. 2006; Hurdu 2012; Kliment et al. 2016). The phytogeographical division of the whole Carpathian ranges was studied by Tasenkevich (Tasenkevich 2004, 2005; cf. Tasenkevich 2011, 2014).

The study area includes the Slovak, Polish, Romanian and Ukrainian Carpathians (Figs. 1 and 2). We omitted the Hainburger Berge (Austria) because of its low maximum altitude up to 480 m a.s.l. and unsuitable conditions for occurrence of the *Triseto-Polygonion* alliance. Existence of this alliance is not mentioned in the Northern Hungarian Mountains (Lengyel et al. 2016), Moravian (Chytrý 2007) and Serbian Carpathians (Aćić et al. 2013). Of the total area of the Carpathians, about 17% is in Slovakia, only 9.3% in Poland, 11% in Ukraine and as much as 50% in Romania. The western margin of the study area is formed by the Javorníky Mts in Slovakia, the northern by the Western and Central Beskids in Poland, the eastern by the Bucegi Mt. in Romania and the southern margin by the Leaota Mt. in Romania. The Ukrainian Carpathians then have an important role as a bridge linking the Western and Southern Carpathians (Kricsfalusy 2013).

The Carpathian climate is temperate-continental, with more extreme manifestations of the continental climate from west to east; Kadlečík (2016) considers that this mountain range acts as a barrier between the harsher continental climate of the east and the milder oceanic climate in the west, boreal in the north and mediterranean in the south. The temperature, precipitation and, wind change with altitude and the high mountain zone ensures a cold and moist climate with mean annual temperatures between +2 °C and -2 °C and annual precipitation from 1800 to 2000 mm in the north-western Carpathians. This then falls to 900–1600 mm in the Eastern, Southern and south-eastern Carpathians. In addition, quaternary glaciation affected only the highest peaks, and the current relief forms were shaped by running water (Kondracki 1978; Ronikier 2011). Geologically, the Carpathians were formed from structural parts situated along the arch and these are still mostly

manifested in various parts of the mountains (Ronikier 2011). They extend in a geologic system of parallel structural ranges, with the flysch sandstone-shale band forming the main Carpathian outer zone. While crystalline and heat-altered metamorphic rocks are present as smaller isolated blocks surrounded by depressed areas which dominate the Southern Carpathians, the accompanying limestone rocks are discontinuous across the range. These features are supported by a rugged chain of volcanic rocks, which form important structural elements in areas such as the Romanian Eastern Carpathians (Kondracki 1978, 1989; Coldea 1991; Ronikier 2011). The soils are determined by the type of parental mountain rock, altitude, and vegetation cover. Brown acid soils and podzols are the most common; brown acid soils dominate the high mountain meadows and podzols predominate in the foothills and inter-montane basins (Uziak 1964).

Data preparation and analyses

Published relevés in the national phytosociological databases and unpublished relevés from private databases provided the source data for evaluating *Triseto-Polygonion* vegetation in the Carpathians. All phytosociological relevés were recorded according to the principles of the standard Central-European method (Zürich-Montpellier school; Braun-Blanquet 1921, 1964; Westhoff and van der Maarel 1973; Van Der Maarel 1975) and stored using TURBOVEG database software (Hennekens and Schaminée 2001). Plots with homogenous species composition and environmental conditions (aspect, slope, micro-relief) were chosen for sampling new recent relevés. Homogenous species composition was represented by clear vegetation type not transitional stages between other associations or alliances (classes). The plot selected for a relevé was choosen as a representative sample of vegetation occurring on a larger area and the species composition was similar across the entire plot.

The initial dataset of 23,965 relevés comprised all accessible published and unpublished relevés of *Molinio-Arrhenatheretea*, *Nardetea strictae* and *Mulgedio-Aconitetea* classes in the study area. We used 9029 relevés from Slovakia (Slovak Vegetation Database, Hegedüšová 2007; Šibík 2012, EU-SK-001 in the Global Index of Vegetation-Plot Databases, private databases of Katarína Hegedüšová, Iveta Škodová and Jana Májeková), 5220 relevés from Poland (Polish Vegetation Database, EU-PL-001, Kacki and Śliwiński 2012; Grasslands in the Polish Carpathian database, EU-PL-002, Korzeniak 2013b, private database of Joanna Korzeniak), 3748 from Romania (Romanian Grassland Database, EU-RO-008, Vasilev et al. 2018, private databases of Albert Reif, Adrian Stoica and Gheorghe Coldea, Cluj) and 5968 relevés from Ukraine (Ukrainian Grasslands Database, EU-UA-001, Kuzemko 2012; Zajac et al. 2016, private database of Vasyl Budzhak and Alla Tukaryuk, Chernivtsi). This initial dataset was processed using JUICE 7.0.194 program (Tichý 2002). Species found in several layers (especially juvenile species of shrubs and trees) were merged into one layer in each relevé. We eliminated relevés unsuitable for analysis from the unstratified dataset in the following steps: i) relevés without plot size and geographical coordinates were excluded from the dataset; ii) relevés which failed the < 4 m² or > 100 m² plot size for grassland vegetation were removed to minimise the negative impact of different plot size on species constancy and dataset homogeneity (Chytrý and Otýpková 2003; Dengler at al. 2009); iii) relevés with more than 25% cover of tree/shrub layers were removed; iv) relevés with altitude less than 600 m a. s. l. were excluded. After these steps, the dataset was thus reduced to 6938 relevés with 1672 taxa.

Relevés with less than four diagnostic species of the *Triseto-Polygonion* alliance according to literary sources (Matuszkiewicz 2007; Solomakha 2008; Coldea 2012; Hegedüšová 2014; the diagnostic species of the alliance are listed in Supplement S4) were excluded. Taxa determined only at the genus level together with cryptogams, woody and shrub species (except *Alchemilla* spec. div.) were excluded prior to analyses. To remove unbalanced distribution of the relevé plots (Knollová et al. 2005), heterogeneity-constrained resampling (Lengyel et al. 2011; Wiser and De Cáceres 2013) was performed. The strata were defined based on the geographical position of individual plots. For each stratum of 1.5' latitude and 2.5' longitude (approximately 2.8×3 km), one to ten plots were

selected. Relevés of the target vegetation unit were selected based on numerical classification using PC-ORD 5.0 software package (McCune and Mefford 1999), with Jaccard Distance Measure and -0.25 Flexible Beta with Square Root Transformation at p = 0.5. Relevés of non-target vegetation units (*Nardetea strictae* and *Mulgedio-Aconitetea* classes) were deleted from the dataset in successive steps. Ordination graphs of preliminary DCA made in Canoco 5 program (Šmilauer and Lepš 2014) were used for visual detection of outliers, which were subsequently excluded from further analyses. These additional provisions established the progressive dataset of 3538 relevés with 1421 taxa.

Semi-supervised K-means

The Slovak expert system for identification of grassland syntaxa (Janišová 2007; Hegedüšová Vantarová and Škodová 2014) was used to set the *a priori* groups in the semi-supervised K-means classification (Tichý et al. 2014) representing typical relevés of clearly delimited associations. The typical relevés of vegetation units of the Triseto-Polygonion alliance delimited in Poland and Romania were selected and approved by phytosociological experts based on Polish and Romanian syntaxonomical literature and added to the *a priori* groups. Also relevés not matching the formal definitions in the Slovak expert system but confirmed by the phytosociological experts as typical relevés were included. The relevés clearly classified as non-target vegetation in the above-mentioned Slovak expert system were removed. These were; associations of Arrhenatherion elatioris, Cynosurion cristati, Deschampsion caespitosae and Poion alpinae alliances. Relevés with over 70% cover of Alopecurus pratensis, Calamagrostis arundinacea, Festuca carpatica, F. picturata, F. rubra and Nardus stricta species were also excluded. After these steps the dataset contained 1,204 relevés and 921 species. A total of 115 relevés in seven a priori groups consisting of six to 29 typical relevés were selected to represent core associations of the target vegetation. Semi-supervised classification including seven a priori groups was used to expand the a priori groups by the relevés most similar to typical relevés. K-means analysis was performed with fixed centroids, three pseudospecies cut-off levels (0%, 5% and 25%) and Hellinger transformation. This classification process was repeated in 15 cycles, and a further 428 relevés were assigned to the seven a priori groups after analysis. To set the final number of distinguished clusters we used semi-supervised K-means analysis again. Following several cycles of K-means with the same parameters as in previous analyses and with a different number of clusters, we set the final number of newly distinguished clusters to two. To verify clusters homogeneity, we used DCA. Outliers of each delimited cluster were excluded from the dataset after expert consideration. The final dataset contained nine groups, 612 relevés and 719 species.

Synoptic table

The synoptic table of the *Triseto-Polygonion* alliance was calculated in JUICE (Tichý 2002). Diagnostic species were determined by the fidelity concept (Bruelheide 1995; Chytrý et al. 2002, 2006; Chytrý and Tichý 2003; Chytrý 2007). Fisher's exact test at P < 0.001 was used to eliminate the fidelity value of species with a non-significant pattern of occurrence. The size of all clusters was standardized to an equal size and the size of each target group was set as 11% of the total data set (Tichý and Chytrý 2006). The critical coefficient phi value for diagnostic species was set as ≥ 0.20 . Among them, only species with a frequency $\geq 20\%$ in particular clusters were adopted in the synoptic table. In the list of diagnostic species, constant species include those present in over 50% of relevés ordered according to species frequency. Dominant species were ordered according to the percentage of relevés in which they reached a cover of more than 25% in at least 5% of relevés. Diagnostic taxa differentiate particular community either by unique occurrence or by a markedly higher frequency. The difference in frequency of differential species was at least 20% and at the same time the species could not be constant (frequency 50% and more) in other units. If a diagnostic taxon was missing in other units of the same rank or had low/nul fidelity, it could reach a lower frequency than 20% in the particular unit.

Compositional variation

The main environmental gradients in the species composition of the *Triseto-Polygonion* alliance were analysed using DCA from the R-project package VEGAN (Okasen et al. 2011) under JUICE. Here, display parameters were sites, spider plots and centroids; cover values were log-transformed and rare species down-weighted. To establish the ecological interpretation of ordination axes, the average combined Ellenberg and Jurko indicator values (IV) for relevés (Jurko 1990; Ellenberg et al. 1992; Šibíková et al. 2010) with the altitude for each relevé were plotted on a DCA ordination diagram as supplementary environmental data. This combination of Ellenberg and Jurko IV was employed because many species present in the mountains in Slovakia, Poland, Ukraine and Romania do not possess Ellenberg's IV. Some species also behave differently in Slovakia than in Germany where Ellenberg's IV were derived; and Jurko's IV were created directly for Slovak flora which is more similar to Ukrainian and Romanian flora. The taxa which had no determined indicator value are listed in Supplement S5. The differences in ecological indicator values, number of vascular plants, altitude and selected climatic variables in the delimited vegetation types were tested by Kruskal-Wallis ANOVA, and multiple comparison tests of the mean ranks were completed using STATISTICA software (StatSoft Inc. 2013) with a critical value of p=0.05. These were expressed in Box and Whisker Plots. Spearman's correlation coefficient was then used to calculate the correlation between 10 selected environmental variables comprising IV, altitude, climatic factors (AMT – annual mean temperature, AP – annual precipitation and TAR – temperature annual range, AP, TAR) and the first two ordination axes. After multiple correlations, Bonferroni correction controlled the familywise error critical value rate of $\alpha = 0.05/12$.

Results

Classification and phytocoenological characteristics of the associations

The semi-supervised classification enabled the final determination of the entire Carpathian dataset. The eight known and one newly well-interpretable associations of the *Triseto-Polygonion* alliance were finally determined and described. The list of occurrences and number of relevés in each syntaxon is then reported in Table 1. The distribution map of the studied alliance and associations in the Carpathians is depicted in Figs. 1, 2 and 3. The synoptic table reveals the differences in floristic composition of each association based on diagnostic, constant and dominant species (Table 2); diagnostic, constant, and dominant species are listed in Supplement S2. The DCA of the 612 relevés featured in Fig. 4 highlights the main environmental gradients in the species composition. The interrelationships of the vegetation units and the number of species, AMT, TAR, AP, altitude and individual environmental factors are then shown in Fig. 5.

Campanulo glomeratae-Geranietum sylvatici Ružičková 2002

(Table 2, Supplement S2, Cluster 1, Figs. 1 and 2, Supplement S6 – Fig. 6/1)

The Campanulo glomeratae-Geranietum sylvatici association is the most xerothermic type of mountain hay meadows in the Carpathians. It represents species-rich multi-layer stands with dominant broad-leaved species (Alchemilla spec. div. and Geranium sylvaticum) together with graminoids (Agrostis capillaris, Arrhenatherum elatius, Bromus erectus, Festuca rubra agg. and Trisetum flavescens) and mesophilous species of the Arrhenatherion elatioris alliance. The thermophilous species indicate the alkaline and warm sites. The cryptogam coverage is very low and only reaches more than 25% at sites with sufficient humidity. The most common are Climacium dendroides, Plagiomnium affine agg., P. cuspidatum and Pleurozium schreberi. The community occurs on warm limestone areas of submontane to montane level (Table 4). The centre of its occurrence is in Slovakia, though we expect a marginal occurrence in Poland and Ukraine. This mountain meadow type is rare today and mainly dependent on abandonment of traditional land use

and it is therefore considered a relic of semi-intensive traditional agriculture (Hegedüšová et al. 2011). It is often accompanied by numerous endangered rare and endemic species (e.g. *Campanula serrata*, *Crocus vernus* subsp. *vernus* and *Lilium bulbiferum*).

Geranio sylvatici-Trisetetum flavescentis Knapp ex Oberd. 1957

(Table 2, Supplement S2, Cluster 2, Figs. 1 and 2, Supplement S6 – Fig. 6/2)

This association is relatively homogeneous, multi-layered and medium species-rich and is dominated by mesophilous species of the Arrhenatherion elatioris alliance combined with medium-tall grasses (Agrostis capillaris, Anthoxanthum odoratum agg. and Trisetum flavescens). The middle layer is dominated by the montane herb Geranium sylvaticum. The relatively abundant ground layer consists of clovers and the shade-tolerant species Alchemilla spec. div., Arabidopsis halleri and Bellis perennis. While Alopecurus pratensis and Lychnis flos-cuculi have higher abundance in humid areas, the nitrophilous species Anthriscus sylvestris, Bellis perennis, Poa trivialis and Schedonorus pratensis together with Trisetum flavescens occupy fertilised meadows. Abandonedt areas or areas with reduced farming activity are dominated by Agrostis capillaris, Briza media, Carex pallescens, Crepis mollis, Festuca rubra agg., Hypericum maculatum and Luzula campestris agg. These meadows occur in localities with specific climatic conditions and long-lasting snow cover predominantly in Slovakia (Table 4). A typical phenomenon is frequent mist and ground night inversion. Scattered stands with similar climatic conditions are also found in the mountain ranges of Poland. Nevertheless, we can expect it also in Romania (Apuseni Mts). To preserve this type of meadows as they were in the past, it is necessary to choose appropriate management practices (mowing once a year and moderate fertilizing).

Crepido mollis-Agrostietum capillaries Ružičková 2004

(Table 2, Supplement S2, Cluster 3, Figs. 1 and 2, Supplement S6 – Fig. 7/3)

Species- rich semi-natural, two- to three-layer grasslands include regularly mowed and occasionally fertilised or recently abandoned mountain meadows and pastures. They are dominated by Agrostis capillaris and Festuca rubra agg. grasses with medium-fodder quality along with the constantly represented species Anthoxanthum odoratum agg. and Dactylis glomerata. While Jacobaea subalpina, Potentilla aurea and Viola lutea have greater frequency at higher altitudes, Alopecurus pratensis, Heracleum sphondylium and Lychnis flos-cuculi can be more abundant on wet and nutrient-rich soils. Trollius europaeus creates here a significant aspect with relatively high coverage. On the contrary, coenoses on nutrient-poor soils are dominated by Hypericum maculatum, Luzula campestris agg., L. luzuloides, Ranunculus polyanthemos and Thymus pulegioides. The middle layer is characterized by the presence of Alchemilla spec. div., Leucanthemum vulgare agg. and Ranunculus acris which require sufficient light. A large quantity of herb layer biomass prevents the development of mosses, the coverage of which usually does not exceed 10%. The most common mosses are Climacium dendroides and Pleurozium schreberi. The occurrence of rare, endangered and endemic species (e.g. Campanula serrata, Crocus vernus subsp. vernus, Gladiolus imbricatus, Gymnadenia conopsea and Trollius europaeus) is also important. The community of Crepido mollis-Agrostietum capillaris inhabits colder and wetter sites on mild slopes (Table 4). The centre of its occurrence is at submontane and montane levels in Slovakia and Poland. Finally, the factors most significantly affecting the floristic composition and the overall structure of these communities are the geographical position, microclimatic features and abandonment.

Geranio-Alchemilletum crinitae Hadač et al. 1969

(Table 2, Supplement S2, Cluster 4, Figs. 1 and 2, Supplement S6 – Fig. 7/4)

These open, homogenous, chionophilous, mostly two-layer montane meadows are species mediumrich. They occur at higher altitudes with long-lasting snow cover and are dominated by broad-leaved species such as Alchemilla spec. div. and Geranium sylvaticum. The stand structure is complemented with flowering herbs (e.g. Bistorta officinalis, Campanula serrata, Crepis mollis, Jacobaea subalpina, Phyteuma spicatum, Pimpinella major, Trollius europaeus and Viola biflora). Grasses Agrostis capillaris, Festuca rubra agg. and Trisetum flavescens up to 60cm high have a high constancy in the upper layer. Depending on the soil chemistry and changes in management, almost monodominant stands of the species Bistorta officinalis or Hypericum maculatum are typical. In the humid places, the species Geranium sylvaticum is replaced by G. phaeum. These species, together with Ligusticum mutellina, Soldanella carpatica and Trollius europaeus, indicate poor leached soils and fallow land, in contrast to Rhinanthus pulcher which indicates regular farming. The moist soils host several hygrophilous species (e.g. Alopecurus pratensis and Geum rivale). The cryptogam layer is poorly developed, with normally less than 20% cover. The most frequent mosses are *Plagiomnium* undulatum and Pleurozium schreberi. The communities of Geranio-Alchemilletum crinitae occur at montane, supramontane to subalpine levels, mostly on moderate slopes (Table 4). Montane meadows with Alchemilla species are valuable not only for the occurrence of endangered, vulnerable and endemic species but also for their unique character. They are endangered due to their abandonment (Rozbrojová et al. 2010; Hegedüšová Vantarová 2014) and also air-pollution (Rusek 1993). Due to abandonment, these stands no longer exist in their previous form. The centre of its occurrence is in Slovakia and marginally in Poland.

Alchemillo-Deschampsietum caespitosae Hadač et al. 1969

(Table 2, Supplement S2, Cluster 5, Figs. 1 and 2, Supplement S6 – Fig. 8/5)

Alchemillo-Deschampsietum caespitosae is a species-poor, closed, monodominant, two-layer, slightly chionophobic, physiognomically striking community with a height up to 100 cm. The association comprises predominantly thick and compact tussocks of Deschampsia cespitosa, with the lower layer dominated by broad-leaved species of Alchemilla spec. div., Geranium sylvaticum, Hypericum maculatum, Jacobaea subalpina and Primula elatior together with Achillea millefolium agg., Campanula serrata, Potentilla aurea and Rumex arifolius. Among the graminoids, Agrostis capillaris, Festuca rubra agg., Luzula luzuloides and Phleum rhaeticum are more constant. Moss coverage is relatively low and does not exceed 15%. The most common are Brachythecium albicans, Pleurozium schreberi and Climacium dendroides. Typical habitats are humid sites on the windward slopes (Table 4), close to saddlebacks and saddleback plains with a slightly undulating concave surface and relatively high (150 cm) snow cover which remains in some areas until the end of May/early June (Bělohlávková 1980). The soil surface usually does not freeze. The stands developed especially after deforestation and these are conditioned by long-term grazing. The centre of its occurrence is at the supramontane level. Finally, the community is relatively common, mainly in the mountains of Slovakia and marginally in Poland, Romania and Ukraine.

Phyteumo (orbicularis)-Trifolietum pratensis Balcerk. 1978

(Table 2, Supplement S2, Cluster 6, Figc. 1 and 2, Supplement S6 – Fig. 8/6)

This association includes low-growing, calciphilous montane grasslands on limestone or dolomite bedrock and is used as meadows and pastures. It is species-rich, colourful and has a high abundance of small and medium-tall plants in the herb layer. The species composition is characterised by codominance of meadow species of the *Molinio-Arrhenatheretea* class and calcareous species of the *Elyno-Seslerietea* class. Another typical feature is the occurrence of thermophilous species (e.g. *Carex caryophyllea, Gentiana cruciata, Helianthemum nummularium* agg. and *Plantago media*). Usually there is no clear dominant. The cryptogam coverage varies and is even up to 70% in some sites; the most common are *Abietinella abietina, Brachythecium mildeanum, B. albicans, Hypnum*

lindbergii and *Plagiomnium cuspidatum*. These grasslands occur predominantly on alluvial fans, with gentle inclination (Balcerkiewicz 1978) at the submontane and montane level, exclusively in the Western Carpathians.

Astrantio-Trisetetum flavescentis Knapp et Knapp ex Oberd. 1957

(Table 2, Supplement S2, Cluster 7, Figs. 1 and 2, Supplement S6 – Fig. 9/7)

These species-rich communities are mostly dominated by *Trisetum flavescens* and *Astrantia major* together with Trollius europaeus. The species Centaurea phrygia agg., Cirsium erisithales and Lotus corniculatus, together with species of the Triseto-Polygonion alliance and mesophilous species of the Molinio-Arrhenatheretea class occur with high frequency. Finally, Alchemilla spec. div. is frequently present as a co-dominant. The stand structure creates conditions for the occurrence of grasses of nutrient-poor sites (Agrostis capillaris, Anthoxanthum odoratum and Festuca rubra agg.) together with frequent occurrence of broad-leaved grasses of more nutrient-rich sites (*Cynosurus cristatus*, Dactylis glomerata and Phleum pratense). Loss of nitrate nutrients after abandonment of traditional farming induced community degradation to phytocoenoses dominated by Agrostis capillaris and Festuca rubra. In the moss layer, species like Rhytidiadelphus squarrosus, Climacium dendroides, Pleurozium schreberi, Plagiomnium undulatum and Calliergonella cuspidata are the most frequent with coverage of 1 to 75%. These communities occur frequently in small areas at the border of deciduous forests on gentle slopes (Table 4), near the villages in the mountain belt at submontane and montane levels. The geological substrate is mostly rich in limestone, which enable the development of soils with a high nutrient content. This vegetation type occurs throughout the entire study area.

Violo declinatae-Agrostietum capillaris ass. nova

(Tables 2 and 3, Supplement S3, Cluster 8, Nomenclatural type: relevé nr. 20, Figs. 1 and 3, Supplement S6 – Fig. 9/8)

This association includes homogenous, species medium-rich, floriferous mountain grasslands. The well developed herb layer (cover 90–100%) is mostly dominated by medium-tall graminoids (Agrostis capillaris, Dactylis glomerata agg., Festuca rubra agg. and Trisetum flavescens) and broad-leaved herbs (Astrantia major, Alchemilla spec. div. and Cirsium erisithales). Viola declinata is the significant diagnostic species of this community. Among the other constant species, there are common species of montane hay meadows (Trollius europaeus, Astrantia major, Campanula serrata and Heracleum sphondylium). This species combination together with Geranium sylvaticum and Pimpinella major corresponds to the Triseto-Polygonion alliance. However, occurrence of some thermophilous species (e.g. Galium verum, Pimpinella saxifraga and Thymus pulegioides) accompanied with species of mesic grasslands of the Arrhenatherion elatioris alliance is very common as well. Abandoned localities are indicated by the occurrence of *Hypericum maculatum*. Species of the Nardetea strictae class (Potentilla erecta, Luzula campestris agg. and L. luzuloides) are also frequent. In contrast, localities with high soil moisture content are indicated by Angelica sylvestris, Crepis paludosa, Deschampsia cespitosa and Myosotis scorpioides agg. The moss layer is slightly developed with coverage up to 5%. There is also typical occurrence of endemic species such as Campanula serrata, Cyanus mollis and Viola declinata together with the Eastern Carpathian species of Centaurea kotschyana, Dianthus barbatus subsp. compactus, Euphorbia carniolica and Podospermum roseum (Kliment et al. 2016). Following the DCA and cluster analysis, two different variants of this vegetation were distinguished (Table 3). The characteristic feature of the first variant typicum is the high species constancy and cover of the Triseto flavescentis-Polygonion bistortae alliance and Molinio-Arrhenatheretea and Festuco-Brometea classes. The second variant with Cirsium erisithales occurs on more humid soils with long-lasting snow cover at higher altitudes (1413–1647 m a.s.l.). The grasslands of *Violo declinatae-Agrostietum capillaris* are typical in the

middle montane belt of submontane, montane and subalpine levels of Ukraine (Table 4). They have intensive agricultural use, being fertilised and now regularly mown. These communities need protection as examples of traditional farming in the Carpathian mountain areas which support grassland diversity conservation.

Trollio altissimi-Knautietum dipsacifoliae Winnicki ex Hegedüšová et al. ass. nov. hoc. loco

Syn.: Trollio altissimi-Knautietum dipsacifoliae Winnicki Monogr. Bieszcz. 4: 102, 1999 (art. 5)

Nomenclatural type: Winnicki 1999, tab. 20, relevé nr. 14, lectotypus hoc loco designatus

Knautia maxima (Opiz) Ortmann = K. dipsacifolia Kreutzer

(Table 2, Supplement S2, Cluster 9, Tab. 20 (Winnicki 1999), Nomenclatural type: relevé nr. 14, Figs. 1 and 2, Supplement S6 – Fig. 10/9)

These grasslands are usually dominated by broad-leaved herbs (Alchemilla spec. div., Astrantia major and Knautia dipsacifolia = maxima) and graminoids (Carex pilosa, Deschampsia cespitosa, Poa chaixii and Trisetum flavescens). The vegetation is multi-layered and dense with overgrowth; therefore, the bryophyte layer is reduced at most sites. There is an important presence of both tall herb species of wet meadows (Geranium palustre, Filipendula ulmaria and Trollius europaeus) and subalpine tall-forbs (Aconitum lasiocarpum, Cirsium waldsteinii, Rumex arifolius and Veratrum album). The phytocoenoses host Pan-Carpathian endemics (Campanula serrata) and subendemics (Cyanus mollis), as well as many Eastern Carpathian plant species (Aconitum lasiocarpum, Aposeris foetida, Centaurea kotschyana, Cirsium waldsteinii, Dianthus barbatus subsp. compactus, Veratrum album and Viola dacica). The high abundance of Hypericum maculatum indicates meadow degradation following cessation of traditional farming (Krahulec et al. 1996; Hegedüšová Vantarová 2014). This type of meadow grows on humid and fertile sites, in local depressions and on slopes with various inclinations (Table 4). The centre of Trollio altissimi-Knautietum dipsacifoliae distribution is in south-eastern Poland. This was previously grazed by oxen but since the complete abandonment of farming in this area after the Second world war it is grazed by deer. Most localities are abandoned, and although this semi-natural origin should endow the mountain meadows with resistance, the longterm lack of management has hastened conversion to tall grasslands with subalpine deciduous shrub communities.

Ordination analysis and ecological characteristics

The DCA scatter plot of individual relevés highlights the distribution of particular vegetation types along the first and second ordination axes (Fig. 4). The selected indicator values for relevés (temperature, moisture, light, soil reaction and nutrients), altitude, climatic variables (annual precipitation – AP, annual mean temperature – AMT and TAR – temperature annual range) and species number were post-hoc correlated with the ordination axes to reveal the main environmental gradients in our data set. The distribution of relevés depicts a continuous ecological transition of associations along the main gradient. The first axis was significantly positively correlated with AP, altitude, moisture and slightly with soil reaction and nutrients; and negatively correlated with AMT, TAR, light and slightly with temperature (Table 5). The main environmental gradient here was related to altitude and precipitation. While the right side of the ordination plot contains relevés which occur at higher altitudes with greater AP – Geranio-Alchemilletum crinitae (cluster 4), Alchemillo-Deschampsietum caespitosae (cluster 5) and Trollio altissimi-Knautietum dipsacifoliae (cluster 9), on the contrary, the left side of the ordination plot is occupied by relevés of the most xerothermic type of mountain hay meadows – Campanulo glomeratae-Geranietum sylvatici (cluster 1) and Phyteumo (orbicularis)-Trifolietum pratensis (cluster 6). These host many termophilous plant species together with Astrantio-Trisetetum flavescentis (cluster 7). The second axis is significantly

negatively correlated with the indicator values for nutrients, moisture and slightly correlated with soil reaction and AP (Table 5). While the chionophobic vegetation of *Geranio sylvatici-Trisetetum flavescentis* (cluster 2) and *Alchemillo-Deschampsietum caespitosae* (cluster 5) grow on moist soils and are shifted along the second axis to the lower part of the ordination space, the stands of *Campanulo glomeratae-Geranietum sylvatici* (cluster 1) and *Violo declinatae-Agrostietum capillaris* (cluster 9) thrive on drier and less fertile soils and are concentrated on the opposite side of the diagram.

The comparison of IVs, climatic variables and altitude highlights the significant differences between associations, especially for altitude, AP and AMT (Fig. 5). The *Geranio-Alchemilletum crinitae*, *Alchemillo-Deschampsietum caespitosae* and *Trollio altissimi-Knautietum dipsacifoliae* associations occur at higher altitudes (1100–1700 m a.s.l.) where AP is significantly higher, AMT is lower and TAR is lower than in other delimited communities. In contrast, the *Campanulo glomeratae-Geranietum sylvatici*, *Geranio sylvatici-Trisetetum flavescentis* and *Crepido mollis-Agrostietum capillaris* grasslands are mostly at lower altitudes (600–1000 m a.s.l.).

While the *Alchemillo-Deschampsietum caespitosae* and *Trollio altissimi-Knautietum dipsacifoliae* communities occupy moist habitats, *Campanulo glomeratae-Geranietum sylvatici* and *Violo declinatae-Agrostietum capillaris* are found on drier stands. Although this latter association grows mainly at higher altitudes, soil humidity establishes it on the left of the ordination diagram (Fig. 4). The last two associations mentioned also have the lowest soil reaction values, and this contrasts significantly with most other communities. These grassland types often occur on sites with soils rich in CaCO₃ formed on calcareous rocks. The comparison of light IV revealed that light availability and use is significantly lower in *Trollio altissimi-Knautietum dipsacifoliae* grasslands than in other delimited communities because the presence of two- to three-layer stands ensures that only shade-tolerant plants can exist in the lowest layer.

Comparison of species number (Fig. 5) showed that *Campanulo glomeratae-Geranietum sylvatici* is the most species-rich hay mountain grassland type, while in *Alchemillo-Deschampsietum caespitosae* and *Trollio altissimi-Knautietum dipsacifoliae* grasslands the species number is the lowest.

Discussion

The present classification includes all known well-differentiated types of mountain hay meadows in the Carpathians. While this classification can be interpreted ecologically based on the selected environmental variables of climatic factors, altitude and IVs, it may not include all influences on grassland diversity because it is closely connected with the quality and availability of data from national databases, as well as with the stage of abandonment, management practice (Rozbrojová et al. 2010; Škodová et al. 2015) and time of origin (Rybníček and Rybníčková 2009).

What does the syntaxonomical revision bring?

The syntaxonomical concept adopted in this paper is largely based on that of Slovakian, Polish, Romanian and Ukrainian phytosociologists (Hegedüšová 2007; Matuszkiewicz 2008; Solomakha 2008; Hegedüšová et al. 2011a; Coldea 2012; Hegedüšová Vantarová 2014; Budzhak et al. 2016) with correction, which resulted from the specific environmental conditions and distribution of vegetation within the Carpathians. Because of some discrepancies between particular syntaxonomical systems of the *Triseto-Polygonion* alliance in the Carpathians, there was a necessity to unify it. Our results correspond with semi-supervised K-means analyses and expert view reflecting the environmental and phytogeographical gradients that influence species composition. We expected more associations than the *a priori* groups defined in our Carpathian dataset. Our classification provides a full overview of the variability of Carpathian mountain hay meadows. We also expected the most xerothermic vegetation type of mountain hay meadows – *Campanulo glomeratae*-

Geranietum sylvatici association with the typical occurrence of a large group of subxerophilous species – on the warm slopes of the Ukrainian and Polish Carpathians. However, only one relevé from each of these countries was assigned to this association. Both these relevés are similar to typical relevés described from Slovakia, but their designation is quite old (Ukraine: 1935, Poland: 1954) and based on our results we cannot confirm that this vegetation type occurs recently in those Carpathian areas. We therefore consider that Campanulo glomeratae-Geranietum sylvatici is a very specific and rare vegetation type occurring exclusively in the central Slovakian mountains.

The Geranio sylvatici-Trisetetum flavescentis association has a wider geographic distribution with its centre of occurrence in Germany (Chytrý 2007; Hegedüšová Vantarová 2014). This association has a more oceanic character. Six of the Polish relevés classified to the second cluster in the final data set were originally assigned to the Gladiolo-Agrostietum association. This indicates that Gladiolo-Agrostietum referred to as the most widespread hay meadow community in the Polish Carpathians (Kornaś 1967) described by Pawłowski et al. (1960) and placed originally to the Arrhenatherion elatioris alliance (Matuszkiewicz 2008), is a very heterogeneous and broadly defined syntaxon with wide altitudinal and ecological amplitude. Due to the diffuse boundaries between syntaxa, classification of this vegetation is even more complex. Moreover, Marschall (1951) and Dierschke (1981) included Gladiolo-Agrostietum in the Triseto-Polygonion alliance in contrast to Uhliarová et al. (2014) who consider it a syntaxonomical synonym for *Poo-Trisetetum flavescentis* in the Arrhenatherion elatioris alliance. In addition, Rozbrojová et al. (2010) reported that this vegetation type is classified in different associations in Slovakia and Poland despite their similar species composition: it is classed as Poo-Trisetetum flavescentis in Slovakia and Gladiolo imbricati-Agrostietum capillaris in Poland. According to the authors, this classification difference is conditioned by state borders rather than by any actual difference in species composition. Uhliarová et al. (2014) also provided a more thorough comparison of both communities in their syntaxonomic revision of Arrhenatherion elatioris. Their comparison also included published data from Germany (Oberdorfer 1983; Dierschke 1997) and Austria (Ellmauer and Mucina 1993) in addition to the phytosociological relevés from Poland (Pawłowski et al. 1960) and Slovakia. The analyses showed considerable species and ecology similarity of Poo-Trisetetum and Gladiolo-Agrostietum typicum associations. Relevés with the occurrence of mountain species (Phleum alpinum, Poa alpina, Rumex arifolius, Jacobaea subalpina, Phyteuma spicatum and Primula elatior) had a closer relationship with plant communities of the Triseto-Polygonion alliance. Our analyses identified that the Polish Gladiolo-Agrostietum capillaris relevés were also included in Crepido mollis-Agrostietum capillaris (19 relevés), Geranio-Alchemilletum crinitae (6 relevés), Alchemillo-Deschampsietum caespitosae (9 relevés) and Astrantio-Trisetetum flavescentis (7 relevés).

Crepido mollis-Agrostietum capillaris represents a transition to the other types of mountain hay meadows (Fig. 4), Campanulo glomeratae-Geranietum sylvatici and Geranio-Alchemilletum crinitae. It also has a close relationship to the Arrhenatherion elatioris and Nardo strictae-Agrostion tenuis alliances (Hadač et al. 1969; Kliment 1994; Ružičková 1997, 2004). In warmer places, mesophilous species of Arrhenatherion elatioris occur and the floristic composition is closely related to Campanulo glomeratae-Geranietum sylvatici, while Geranio-Alchemilletum crinitae is a contact phytocoenosis at higher altitudes. In addition, stands where traditional farming methods have been abandoned gradually pass into the Nardo strictae-Agrostion tenuis or Violion caninae communities (Hadač et al. 1969; Kliment 1994; Ružičková 1997, 2004) and at higher altitudes into the Poion alpinae association (Hegedüšová Vantarová 2014). Our analyses confirm that this association also occurs in Poland, with up to 26% of Polish relevés in this association originally assigned to the warmer Gladiolo-Agrostietum. However, we cannot include in the Crepido mollis-Agrostietum capillaris association the phytocoenosis from south-western Ukraine described by Budzhak et al. (2016) because of the lack of association and alliance diagnostic species. Moreover, the Molinia caerulea s. str. species has very high abundance here and these stands have close relationship to the Calthion alliance.

The Geranio-Alchemilletum crinitae association has a very close syngenetic relationship with Alchemillo-Deschampsietum caespitosae and Mulgedio-Aconitetea communities; proven by the presence of Rumex arifolius, Gentiana asclepiadea, Ligusticum mutellina, Primula elatior, Jacobaea subalpina, Silene dioica and Veratrum lobelianum species (Hegedüšová Vantarová 2014) and similar ecological contidions (same biotopes in higher altitudes). With these communities, there are continuous transitions clearly distinguished in the field. The type of management and site of occurrence also affect variability in association species composition (Kliment 1994; Ružičková 1997). Our analyses also confirmed their occurrence in Poland and documented in the Western Tatras by relevés research performed after 2000. Finally, although Malynovskyy (1980), Malynovskyy and Kricsfalusy (2000) and Prots and Kagalo (2012) mentioned these communities in Ukraine, our analysis did not confirm their presence.

The common cluster feature representing Alchemillo-Deschampsietum caespitosae vegetation is a transitional position to Geranio-Alchemilletum crinitae, Phleo alpini-Deschampsietum caespitosae, Rhodiolo-Deschampsietum caespitosae, Aconitetum firmi (Trisetion fusci alliances) and communities of the Adenostylion alliariae alliance. The floristic composition also encourages the conclusion that the association has a very close syngenetic relationship with Nardion strictae, and that it has gradual transitions to this on exposed and unprotected slopes. Further, stand species composition reflects the various ecological conditions and is visible in the form of transitions with contact phytocoenoses. The heterogeneity of this type of vegetation is best explained by the physiogeographical parameters of altitude, slope and aspect together with snow cover thickness and humidity ratios. While Hegedüšová and Ružičková (2007) recorded Alchemillo-Deschampsietum caespitosae as a syntaxonomical synonym for the Geranio-Alchemilletum crinitae association, Hegedüšová Vantarová (2014) now lists it separately due to its clear physiognomic distinctness confirmed by phytosociological relevés as well as the ecological requirements that enable it to dominate Deschampsia caespitosa. Our analyses also confirmed its occurrence in Poland, Ukraine and Romania. The Polish relevés were originally assigned to Gladiolo-Agrostietum alpinetosum (Tatra Mts, Pawłowski et al. 1960) and Gladiolo-Agrostietum deschampsietosum (Gorce Mts, Kornaś and Medwecka-Kornaś 1967). Both associations are considered as sub-associations of Gladiolo-Agrostietum at higher altitudes and relicts of previous traditional sheep farming. The Romanian relevés were previously assigned to *Deschampsion caespitosae* Horvatić 1930 by Puşcaru et al. (1956), Buia (1962) and Sanda et al. (1977). However, this alliance includes alluvial meadows at low altitudes characterised by the absence of montane species and specific ecological conditions. Additional assignments of Alchemillo-Deschampsietum caespitosae relevés were to Calamagrostion villosae by Stancu (2005), Agrostion stoloniferae by Neblea (2006) and to the Adenostylion alliariae alliance by Coldea (1990). Based on our analyses and the occurrence of *Triseto-Polygonion* species, we corrected these previous classifications – noting also that the relevés from the Ukrainian Chyvchyny Mts were not originally assigned to any syntaxa.

Phyteumo (orbicularis)-Trifolietum pratensis was described by Balcerkiewicz (1978) from Polana Chocholowska in the Polish Western Tatras. Although Hegedüšová Vantarová (2014) does not identify this community in Slovakia, our analyses confirmed its Slovak occurrence in the Chočské vrchy Mts, Malá Fatra Mts, Muránska planina plain, Nízke Tatry Mts, Slovenský raj Mt. and Veľká Fatra Mts due to both similar ecological conditions and species composition (Supp. 1). These relevés were not previously clearly assigned to any syntaxa (Bosáčková ined., Ujházy ined., Uhliarová ined., Ružičková ined.) or they were included in Anthoxantho-Agrostietum tenuis (Dzubinová 1978, 1984).

The centre of occurrence of *Astrantio-Trisetetum flavescentis* is in the Alps from where it was originally described (Dutoit 1924; Knapp and Knapp 1952; Oberdorfer 1957; Ellmauer 1995). From Slovakia, Poland and Ukraine, this community has not been mentioned until now. This association has a close relationship with the newly described Ukrainian *Violo declinatae-Agrostietum capillaris* association stands highlighted in Fig. 4. In comparison to other relevés from Slovakia, Poland and

Ukraine, the species *Astrantia major* has a higher abundance. Its dominance of Slovak vegetation is typical at both abandoned sites and those with changed management (Ružičková 1997). In addition, this vegetation type was previously assigned to *Geranio-Alchemilletum crinitae* based on species similarity (Hegedüšová Vantarová 2014).

Violo declinatae-Agrostietum capillaries, a new association, is typical only for Ukraine. This vegetation is floristically very homogeneous with a close relationship to Campanulo glomeratae-Geranietum sylvatici and Astrantio-Trisetetum flavescentis sharing thermophilous species.

Trollio altissimi-Knautietum dipsacifoliae was first described by Winnicki (1999) from the Bieszczady Mts as the tall-forb community Trollio altissimi-Knautietum dipsacifoliae Winnicki 1999 and classified to the Adenostylion alliariae alliance, Betulo-Adenostyletea (=Mulgedio-Aconitetea) class (Winnicki 1999). Iakushenko et al. (2012) then classified it as a syntaxonomical synonym of Poo chaixii-Deschampsietum cespitosae Pawłowski et Walas 1949 (Mulgedio-Aconitetea class). Comparing the diagnostic species of both communities, we decided to transfer Trollio altissimi-Knautietum dipsacifoliae to Triseto-Polygonion (Molinio-Arrhenatheretea class) instead of its traditional classification in the Adenostylion alliariae (Winnicki 1999) or Calamagrostion villosae (Iakushenko et al. 2012) alliances. According to semi-supervised analyses, relevés of Polish Trollio altissimi-Knautietum dipsacifoliae have a very close relationship with Astrantio-Trisetetum flavescentis and Geranio-Alchemilletum crinitae and have an intermediate position between them (Fig. 4). This analysis is based on similar stand species composition and the content of the following Triseto-Polygonion species: Arabidopsis halleri, Astrantia major, Campanula serrata, Heracleum sphondylium, Phyteuma spicatum and Trollius altissimus. However, Winnicki (1999) did not assign a nomenclatural type for Trollio altissimi-Knautietum dipsacifoliae and therefore its name is not considered valid. For validation, we chose relevé number 14 recorded in Table 20. The approved valid name is now Trollio altissimi-Knautietum maximae Winnicki ex Hegedüšová et al. ass. nov. hoc. loco.

K-means classification; advantages and limitations

Semi-supervised classification which formally reproduces the existing units in a supervised mode, and simultaneously identifies new units at unassigned sites in an unsupervised mode, is increasing in popularity and is currently used in several national and supra-national classification studies (Rodríguez-Rojo et al. 2014; Slezák et al. 2014; Tichý et al. 2014; De Cáceres et al. 2015; Smale and Wiser 2015; Wiser et al. 2015; Douda et al. 2016; Janišová et al. 2016; Kuzemko 2016; Zajac et al. 2016; Wiser and De Cáceres 2018).

We decided to use semi-supervised K-means classification instead of the common unsupervised and supervised methods mainly because of i) the heterogeneity of the initial dataset in the large Carpathian area and ii) our assumption that some Slovak, Romanian and Polish associations of the *Triseto-Polygonion* alliance exist also in other parts of the Carpathians, which we eventually confirmed.

We applied the revised classification of Slovakia (Electronic Expert System: Janišová 2007; Hegedüšová Vantarová and Škodová 2014) to assess *a priori* groups. However, this approach was preferentially developed for Slovakian territory, and we therefore performed an additional expert revision of typical relevés of *a priori* groups because final clusters have greater homogeneity when the *a priori* groups have more relevés (Zajac et al. 2016). The intermediate step extended *a priori* groups by semi-supervised k-means analysis with fixed centroids. Both classifications with fixed and non-fixed centroids were tested but similar to previous studies (Zajac et al. 2016) classification with non-fixed centroids provides more heterogeneous clusters.

An indisputable advantage of semi-supervised classification is the identification of new units (Tichý et al. 2014). We identified one new unit *Violo declinatae-Agrostietum capillaris* and confirmed *Trollio altissimi-Knautietum dipsacifoliae* previously described by Winnicki (1999) within the *Mulgedio-Aconitetea* class. Moreover, we finally confirmed that identical or similar vegetation units occur in all Carpathian countries. In the case of Polish *Triseto-Polygonion* classification, we verified the occurrence of five extra associations in addition to the recognised *Phyteumo (orbicularis)-Trifolietum pratensis* (Matuszkiewicz 2008). Based on our results of semi-supervised classification we can conclude that there are also mountain grasslands of the *Triseto-Polygonion* alliance in some parts of the Ukrainian Carpathians where its occurrence was previously uncertain and controversial (Solomakha 2008; Škodová et al. 2015; Budzhak et al. 2016; Zajac et al. 2016). Further, the semi-supervised classification of vegetation data from the neighbouring Carpathian countries enabled syntaxa standardisation throughout the region and this proved successful in a supra-national classification.

This approach, however, is limited by the high percentage of unassigned relevés in the dataset because only 612 of the initial 1204 relevés were classified to known and new units. Although this contrasts with Zajac et al. (2016) classification of the majority of relevés in the final selected dataset, it was an expected result due to the high heterogeneity of Carpathian mountain hay meadows and theirs differences in substrate, altitude, exposition, land use, etc. The remaining 592 relevés were classified by relevé authors and also by Expert systems as Arrhenatherion (Poo-Trisetetum, Gladiolo-Agrostietum in Poland), Cynosurion, Nardo strictae-Agrostion, Poion alpinae and Mulgedio-Aconitetea class which are contact phytocoenoses of the Triseto-Polygonion alliance. A few relevés might belong to Triseto-Polygonion but most of them are transitional types between Triseto-Polygonion, Arrhenatherion and Nardo strictae-Agrostion alliances and it is hard to classify them to particular associations of these alliances. This has also been discussed by Ružičková (2002). Additional problems encountered were the multiple methods used in data collection, and different national syntaxonomical systems used to classify them, as well as the large time span of data collection.

In conclusion, our study supported the previous findings by Tichý (2014), Kuzemko (2016) and Zajac et al. (2016) that the semi-supervised method is an appropriate tool for vegetation syntaxonomical classification at the supra-national level.

Compositional variation – the most important environmental factors

DCA correlates the major compositional gradient primarily with altitude and precipitation, and this is consistent with the results of several other studies (Lososová et al. 2004; Bruelheide and Jandt 2007; Prach et al. 2007; Janišová et al 2010; Hanzlik and Gerowitt 2011; Pal et al. 2013; Škodová et al. 2015). The Polish and Slovak mountains have a more oceanic climate, with a relatively high rainfall, which could be unfavourable for the development of *Astrantio-Trisetetum flavescentis* and *Violo declinatae-Agrostietum capillaries* association. While communities with *Astrantia major* in Poland and Slovakia only occur on sites with specific ecological conditions induced by abandonment (Ružičková 1997; Zarzycki 2008), there is no existence of *Violo declinatae-Agrostietum capillaris* recorded in these countries. Distribution of this association appears to be concentrated predominantly in the more continental climate parts of the Ukraine Carpathians. However, EIJV for continentality was excluded from all analyses, because the study area (Fig. 1) is geographically limited to reflect its effect. By contrast, Hegedüšová and Senko (2011) declare that the main compositional gradient of Slovakian mountain hay meadows correlates with moisture and nutrient availability. Differences in opinion here may be due to different study area sizes and consequent specific geological substrata, soil and climatic conditions.

Plant species richness in mountain areas is generally considered to decrease with increasing altitude. This has also been discussed by Stevens (1992), Körner (2000), Theurillat et al. (2003) and

Boscutti et al. (2018). It clearly supports our results, where *Campanulo glomeratae-Geranietum sylvatici* is the most species-rich community and it occurs at a lower altitude contrary of the higheraltitude and significantly less species-rich *Alchemillo-Deschampsietum caespitosae*, *Geranio-Alchemilletum crinitae* and *Trollio altissimi-Knautietum dipsacifoliae* communities (Figs. 4 and 5). Moreover, precipitation increases with increasing altitude and annual mean temperature decreases, with the result that higher moisture and cooler temperatures at higher altitudes particularly influence soil properties, producing a general decrease in nutrients and pH with increasing altitude (Strong et al. 2011; Škodová et al. 2015; Zajac et al. 2016; Mardari et al. 2019). This implies that among the abiotic habitat conditions, nutrient content is also important for species richness in the studied grasslands. Nevertheless, it is obvious that the nutrient content may depend both on management and productivity (Poldini et al. 2011; Gillet et al. 2016; Brun et al. 2019) as well as on environmental factors.

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Author contributions

KH designed the study and compiled the manuscript; KH, IŠ, JK, JM, conducted the phytosociological sampling; KH and IŠ performed the statistical analyses; KH, JK, AS, GC, VB, AT and IC have provide unpublished relevés; JM has prepared maps; KH coordinated the manuscript compilation; IŠ, JK, AS and AK revised and completed some parts of manuscript and all the authors commented on the manuscript.

Declaration of interest statement

The authors declare that they have no conflict of interest.

Taxonomic references: The taxonomic nomenclature for vascular plants followed Euro+Med Plant Database (Euro+Med 2015) (http://ww2.bgbm.org/EuroPlusMed/query.asp). The names of missing taxa were according to Flora Europaea (Tutin et al. 1968-1993). The nomenclature of non-vascular plants was in accordance with Marhold and Hindák (1998). Narrowly defined species and subspecies which were not distinguished in the older literature or may have been incorrectly determined, were unified into a broader concept of species aggregates (agg., Supplement S1) according to Marhold and Hindák (1998).

Syntaxonomic reference: The nomenclature of syntaxa is unified as in Hegedűsová Vantarová and Škodová (2014).

Abbreviations: AMT – annual mean temperature, AP – annual precipitation, TAR – temperature annual range; DCA – Detrended Correspondence Analysis; AK – Anna Kuzemko, AS – Adrian Stoica, AT – Alla Tokaryuk, GC – Gheorghe Coldea, IC – Illya Chorney, IŠ – Iveta Škodová, JK – Joanna Korzeniak, JM – Jana Májeková, KH – Katarína Hegedüšová, VB – Vasyl Budzhak; PL – Poland; RO – Romania; SK – Slovakia; UA – Ukraine.

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Acces 6

Table 1. Syntaxonomical affiliation of the associations of Carpathian *Triseto-Polygonion* alliance combined with the list of occurrence and number of relevés in each syntaxon. SK – Slovakia, PL – Poland, UA – Ukraine, RO – Romania.

Cluster	Syntaxonomical affiliation	Country code
No.		(No. of Relevés)
Molinio-Ar	rhenatheretea R. Tx. 1937 em. 1970	
Poo alpin	ae-Trisetetalia Ellmauer et Mucina 1993	
Polygon	o bistortae-Trisetion flavescentis BrBl. et R. Tx.	
ex Marsi	hall 1947	
1. Camp	anulo glomeratae-Geranietum sylvatici Ružičková 2002	SK (46), PL (1), UA (1)
2. Gerar	nio sylvatici-Trisetetum flavescentis Knapp ex Oberd. 1957	SK (36), PL (6), RO (1)
3. Crepi	do mollis-Agrostietum capillaris Ružičková 2004	SK (84), PL (30)
4. Gerar	nio-Alchemilletum crinitae Hadač et al. 1969	SK (133), PL (11), UA (1
5. Alche	millo-Deschampsietum caespitosae Hadač et al. 1969	SK (43), PL (22), UA
		(10), RO (15)
6. Phyte	umo (orbicularis)-Trifolietum pratensis Balcerk. 1978	SK (23), PL (14)
7. Astrai	ntio-Trisetetum flavescentis Knapp et Knapp ex Oberd. 1957	SK (6), PL (13), UA (2),
		RO (49)
8. Violo	declinatae-Agrostietum capillaris ass. nova	UA (40)

PL (27)

9. Trollio altissimi-Knautietum dipsacifoliae Winnicki 1999

Table 2: Shortened synoptic table of *Triseto-Polygonion* alliance based on the semi-supervised classification. Percentage frequency and modified fidelity index *phi* coefficient (as upper index) are displayed. Diagnostic species (DS) of particular clusters are ranked by decreasing frequency to each cluster. Diagnostic species (DS) with fidelity value equal or higher than 0.20 and frequency value equal or higher than 0.20 (Fisher's exact test p <0.001) are on a grey background. Only species with frequency $\geq 10\%$ were included to the "Other abundant species". *Crocus vernus* subsp. *vernus* – *Crocus *vernus*, *Dianthus barbatus* subsp. *compactus* – *Dianthus *compactus*, *Hieracium flagellare* subsp. *flagellare* – *Hieracium *flagellare*, *Ranunculus polyanthemos* subsp. *nemorosus* – *Ranunculus *nemorosus*, *Sesleria sadlerana* subsp. tatrae – Sesleria *tatrae.

Group No.	1	2	3	4	5	6	7	8	9
Association	Cg-Gs	Gs-Tf	Cm-Ac	G-Ac	A-Dc	Po-Tp	A-Tf	Vd-Ac	Ta-Kd
No. of relevés	48	43	114	143	90	37	70	40	27
Avverage no. of species per relevés	67	39	46	33	27	46	41	39	26
Polygono-Trisetion									
Geranium sylvaticum	83 28.4	91 33.7	25	99 39.3	41	8	10	28	7
Pimpinella major	79 34.4	44	21	49 10.0	13	22	53	38	
Campanula serrata	79 29.5	9	16	57 13.6	28	24	20	80 30.1	33
Heracleum sphondylium	42	58	31	62 15.3	20	11	30	78 26.3	37
Crocus *vernus	33 1/.0	35 18.5	18	1	16	27	13	-	14.55
Phyteuma spicatum	31	72 35.0	53 19.6	26	18	24	11	-	⇒15
Astrantia major	23	7	22	40	11	22	100 38.4	92 44.4	96 45.7
Arabidopsis halleri	17	51	51 14.3	9	29	54 16.7	23	2	52
Trollius europaeus	8	9	13	31	4	16	50 14.4	92 46.8	56
DS Campanulo glomeratae-Geranietum syl	vatici								
Tragopogon pratensis agg.	88 46.5	19	35	22		46	20	10	15
Silene vulgaris	75 33.4	7	4	3	6	8	10	8	30
Dianthus carthusianorum agg.	73 59.6	2	11	13	222	24	1	2	
Knautia arvensis agg.	73 40.4	19	34	13	2	30	29	18	
Galium mollugo agg.	69 34.9	30	31	25	2	35	31	20000	7
Arrhenatherum elatius	60 45.4	26	18	3	-	22 1	4	5772	
Trifolium montanum	54 37.4		26 10.3	8	-	32	10	10	172-0
Polygala vulgaris	48 31.4	12	25 8.7	3	4	19	21	12	
Potentilla heptaphylla	46 34.6	2	3	200		11		100000	3575
Anthyllis vulneraria	46 31.3	9	18	5		30	13	10	
Sanguisorba minor	44 46.9	2	6		-	16	3		
Lilium bulbiferum	40 34.7	2	1	0.00	7.75	3	1	55576	
Fragaria vesca	35 33.2	7	10	3	4	3	1	15	
Arabis hirsuta agg.	21 29.3	2		1		11	3		
Salvia pratensis	21 28.3	2	4	7	10000	11	1		
Aquilegia vulgaris	19 26.7	120 C22	9	7	-	5	1		
DS Geranio sylvatici-Trisetetum flaves				1			_		
Silene flos-cuculi	2	67 56.5	28 15.4	0	3	5	3	2	
Alopecurus pratensis	2	58 46.0	19	10	22	5	3	2	3577
Myosotis scorpioides agg.	10	53 20.2	35	21	19	38	27	32	15
Anthriscus sylvestris	6	35 41.8	5	1			9		
Bellis perennis	2	26 48.9	3//	73 1	2	16	9	90703	107570
DS Crepido mollis-Agrostietum capillar	3.3				250	17.00	15		
Crepis mollis	33	40	189 43.8	55 17.8	11	38	16		
Luzula campestris agg.	40	53	68 27.1	17	21	38	30	25	2355
nurura campestris ayy.			00	- 10	21	30	30	23	

VCC66/6/2

					823			9350	222			
DS Geranio-Alchemilletum crinitae	20						45 30.0				2	
Geum rivale	4	93/8	14		19		38 25.1	12	14	10		15
Ranunculus *nemorosus	8		2		8		35 **.*	10	3	3	8	37
Viola biflora			2		4		27 30.0	14			0.55	
Soldanella carpatica	4 2		2		2		22 **	10	5	1		
Cirsium eriophorum	1.72				2		22	10	5			
DS Alchemillo-Deschampsietum caespitosae Phleum alpinum			5	***	7	-	5	43 ***.1	8	1	2	555
Bistorta officinalis			16		7	200	21	37 20.5	11	3	2	3.23
Rumex alpinus			10	-	1 -	-	1	20 34.1	5			
Carex leporina			2	10000	8	100	1	20 31.1	S		-	322
DS Phyteumo (orbicularis) -Trifolietum pr	ator	010	-					20				
Trifolium pratense	73	1010	77	-	74 ***	. 3	43	23	97 34.4	69	22	4
Phyteuma orbiculare	29	-	5		16	-	13	6	89 ***	4	2	
Poe elpine	4	0.50	350	1000	3 -	5900	4	12	35 40.5	1	3210145	3177
Thymus pulcherrimus	2				2.00	-	3	6	22 22.8			
Polygala amara agg.	6	55.5		2000	2 -	265	1	1	22 34.4	3	35000	277
Campanula rotundifolia agg.	4				4		5	7	22 ****			
Silene dioica	10	550	12	(983	4	199	3	8	22 ****	1	8	200
Pilosella lactucella						-	1		19 42.5			
Carex flacca				200	4	333	3		19 30.4	4		50.00
Ranunculus breyninus							1	2	19 34.0	1000	5	
DS Astrantio-Trisetetum flavescentis									-			
Cynosurus cristatus	12		19		17		5	2	38	59 34.7	25	
Viola dacica	2	1	2	77.53	858	565	170.00	8777	550	21 41.0	87815	19
DS Violo declinatae-Agrostietum capillar	is a	ss. r	ova							10000000	00	
Angelica sylvestris	4	377	5	5355	4		5		157	4	65 **-	11
Lotus ucrainicus				222	1000	-10	2500-22	1		1	55 1004	
Trifolium alpestre	2				1 -		00	1		4	55 00.3	<u> </u>
Stachys officinalis	4				4		3		5	10	48 24.0	
Centaurea jacea	2		7	22	19 -		1	4	3	16	45 38.7	7
Hieracium umbellatum					52					1	40	7
Trifolium pannonicum		333								4	38 33.4	
Galium verum agg.	2		2		12		1	6	8	6	38 3/-0	
Stachys alpina	2			200				1	100	- B	28 ***	833
Cyanus mollis		5220		222	94		1022	1	17/2	1	25 30.1	11
Achillea carpatica								4		7 ~	22 39.1	
Viola declinata	0.73101				(5)		808	10 ****		10000	22 33.0	(3)33
DS Trollio altissimi-Knautietum dipsacif		le_					20 0.4					100 00.4
Knautia dipsacifolia = maxima	23		122	200			20	9	-	3		
Poa chaixii	8		5	-	41 4/-		34	20	8	6	8	63 33.8
Carex pilosa					2			A		17 10.1	2 - 2 - 2 - 2	56 '4.5 56 57.5
Aposeris foetida			~		55 4 555 			3		11	25 ****	56 */
Filipendula ulmaria	2		9	200	17		6	2		3250 CB 3 1 1 5 1 5	2	48 30.0
Gentiana asclepiadea	12		2		18 °-	400	16	2	3	16	5	44 31-3
Trifolium medium agg.	12		-	222	10			1	3	10	٠	33 33.5
Cirsium waldsteinii Centaurea kotschyana	2			men.	3,46					1 -	15 14.0	33 41.5
Veratrum album	4		2	222	4 -		10 -	7	3	3	15	33 33.4
Aconitum lasiocarpum	7		2	***	7		10		3	3	-	30 24.4
Tussilago farfara	4		5		3		3	2222	3	1		30 31.0
Idsaliago lallara	7		9		3.00		9/		3	1		30
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# <u>####################################</u>	222		77 (2013-14)	10 (200)	2044		2010 2001	10_000000	
Crepis paludosa			4	3	4	1,000	14	8	30 31.4
Geranium palustre			222	222			222		20
Lathyrus laevigatus									19 41.0
Diagnostic species common for two or more	associa	tions							
Colchicum autumnale 8	3 *1.0	12	38	13	2	57 20.0	60 43.4	2	
Campanula glomerata agg. 10		2	5	27	12	14	33	80 34-7	48
Trisetum flavescens 8		98 30.8	40	34	8	32	80 40.4	28	81
Centaurea phrygia agg. 7	1 34.4	23	28	13	7	41	60 ****	25	4
Plantago media 5	6 23.0	19	31	6	6	78 *0.6	37	12	
Linum catharticum 4	8 ****	5	13	2		62 ****	37 ****	25	577
Cirsium erisithales 4	2 41.0	2	12	17	4	22	44 **	20	
Rumex acetosa 5	8	91 24.0	74 40.7	17	10	59	67 ****	25	575
Campanula patula 4	0	77 34.4	76 **-	13	12	41	37	28	
Crepis biennis 2	7	42 **	8	1		11	34 ***	42 **	F - 333
Deschampsia cespitosa	4 "	21	46	76 24.2	100 41.2	32	10	18	74
Rumex arifolius 1	0	7	17	65 33.0	49 ****	5	17	12	26
Jacobaea subalpina	2	30	21	64 31.3	50 40.4	19	3	1018011-122-01	2008 577
Lathyrus pratensis 6		37	39	32	10	14	11	70 ****	70 **-
Tanacetum corymbosum 4	4 4.5		18	22	7	19	7	65 **-*	70
Dianthus *compactus					2		1	32 35.7	26 28.5
Other abundant species with frequency ≥ 10	in at	least on	e cluster					W. C.	
Alchemilla spec. div. 8	3	95	95	100 24.2	90	84	87	42	96
Agrostis capillaris 7		67	100 ****	80	69	59	73	82	70
Hypericum maculatum 7		58	89 **.*	90	74	41	80	62	85
Achillea millefolium agg. 8		70	79	55	64	84	66	65	70
Cruciata glabra 9		81	91 20.3	63	32	51	43	65	52
Festuca rubra agg. 7	3	49	93 **-	49	56	78	73	45	41
Veronica chamaedrys agg. 5		88 **-*	81 ****	49	56	68	66	38	22
Ranunculus acris 5		88 **	95 **-*	27	48	84 **-*	70	15	7
Primula elatior 6		28	64	72 **-0	30	86 ****	46	18	78
Lotus corniculatus agg. 8		40	60 7.8	37	4	51	74 19.4	65 12.1	4
Taraxacum sect. Ruderalia 5		81 33.4	31	15	24	54	56 ****	8	4
Carlina acaulis 8		9	45	19	8	51	34	42	4
Leucanthemum vulgare agg. 8	3 **	65	81 ****	28	13	59	80 10.1	70	1100
Anthoxenthum odoratum agg. 6		84 ***	74	23	37	59	70	45	4
Leontodon hispidus 9		72	54	42	31	84 ***	54	38	
Dactylis glomerata agg. 8	5 24.5	74 18.7	61	36	11	68	53	65	4
Stellaria graminea 4	6	56	75 **	36	30	32	67 ****	62	(X 222)
Trifolium repens 5	8	86 40.0	68 ****	15	30	86 43-4	74 */	30	
Briza media 8	1 43.9	30	68 **-*	26	8	89 ****	40	52	33
Luzula luzuloides 3		16	62 ****	45	42	19	19	30	74 40.4
Vicia cracca agg. 6		51	64 ****	31	6	35	54	25	15
Potentilla aurea 2	5	21	43	48 14.9	64 21.4	38	14	5	4
Schedonorus pratensis 6		47	43	19	17	57	59 ****	45	4
Rhinanthus minor 4		40	61 -0.0	12	4	70 43-1	51	60 ****	
Plantago lanceolata 6	5 **-*	44	61 **-3	4	3	57	61 **	32	955
Carum carvi 5		56 15.0	46 0.0	10	18	59 20.3	50 **-3	22	
Potentilla erecta 2	5	21	63 22.3	10	11	38	30	50	52
Prunella vulgaris 5	6 11.4	30	39 -	11	11	62 **-0	56 ****	30	4
Cerastium fontanum agg. 3	8	51	38	16	30	46	40	10	10.00
Thymus pulegioides 6	2 44.4	14	39	14	7	51	27	52	4
(C)				100					
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Poe pretensis agg. Phleum pratense Carex pallescens Vicia sepium Ranunculus polyanthemos Chaerophyllum hirsutum Gymnadenia conopsea Nardus stricta Ajuga reptans Poe trivialis Pimpinella saxifraga agg. Galium pumilum agg. Ranunculus auricomus agg. Rhinanthus angustifolius Cardamine pratensis agg. Avenula pubescens Ranunculus repens Euphrasia rostkoviana agg. Vaccinium myrtillus Veronica officinalis Ligusticum mutellina Pilosella eurantiaca Senecio nemorensis agg. Traunsteinera globosa Viola tricolor Phleum hirsutum Chaerophyllum aromaticum Helictochloa planiculmis Viola canina Luzula sylvatica Parnassia palustris Neottia ovata Medicago lupulina Achillea distans agg. Myosotis sylvatica agg. Crepis conyzifolia Phleum rhaeticum Avenella flexuosa Geranium phaeum Calamagrostis arundinacea Scabiosa lucida Agrostis stolonifera agg. Epilobium alpestre Taraxacum species Campanula persicifolia Homogyne alpina Carex caryophyllea Gladiolus imbricatus Pilosella officinarum Botrychium lunaria Cirsium arvense	62 4 23 23 23 23 23 23 23 23 21 21 21 21 21 21 21 21 21 21 22 23 23.6 6 2 23 23.6 6 2	19 — 49 16 — 9 — 12 — 9 — 35 14 — 30 19 — 12 — 19 — 2 — 2 — 2 — 2 — 2 — 2 — 2 — 2 — 2 —	40 mm 3 mm	12	24 — 6 — 8 — 10 — 7 — 24 — 1 — 20 — 1 — 1 — 21 — 1 — 1 — 1 — 1 — 1 — 1 — 1 — 1 — 1 —	43	29	5 — 60 32 — 2 — 2 — 15 — 15 — 15 — 12 — 12 — 12	11
	, C	30							

Hypochaeris uniflora Scorzoneroides autumnalis Carex sempervirens Helianthemum nummularium agg. Rhinanthus alpinus Laserpitium latifolium Viola lutea Gentianella lutescens Vicia sylvatica Podospermum roseum Cirsium rivulare Euphorbia amygdaloides Hypericum perforatum Solidago virgaurea Urtica dioica Scabiosa columbaria Holcus lanatus Carex panicea Geum montanum Polygonatum verticillatum Anemone nemorosa Sesleria *tatrae Medicago falcata Thesium alpinum Clinopodium vulgare Luzula sudetica Primula veris Equisetum arvense Leucanthemum rotundifolium Cuscuta species Geranium pratense Salvia verticillata Ranunculus lanuginosus Brachypodium pinnatum Viola hirta	4 — — — — — — — — — — — — — — — — — — —	9 2 9 9 9 5 7 2 2 12 12 12 2 2 2 2	10	3	2 — 8 — 1 — 1 — 8 — 1 — 1 — 1 — 1 — 1 — 1	16	9 3 11 13 17 -	15 — 2 — 8 — — 18 — — 10 — 20 40 — 2 — 5 — 2 — 5 — 10 — 118 40 — 15 40	15
Viola hirta Origanum vulgare	8	2		1	2	744	-	18 30.4	
Euphorbia carniolica	2	2,			<u> </u>		7	12 21.5	
Securigera varia Thalictrum aquilegiifolium	15 20-1	5	2	1	575%	5		12 **.*	3 7.7.3 33
Poa nemoralis	2		*****	1				20 -0.0	
Euphrasia stricta agg. Campanula rapunculoides	2		1	1	, 🖈	4 Z	10 **-	12 **	
Dianthus superbus	1. 311		-	4	-	-	1	10	
Lilium martagon	10 **-3	2	2	1	72		1	10	4
Digitalis grandiflora Taraxacum sect. Alpestria	10	۷			2	16 30.4			
Bromus monocladus	10 49.3		1			3			-
Carduus glaucinus Succisa pratensis	10 207		1			3	1	12 30.4	
Festuca carpatica				1 7		14 34.3		12	
Pedicularis verticillata				4	1	14			
				10000					
Hieracium prenanthoides Ononis arvensis		2	S S	2			1 10	44.4	_11
Hieracium *flagellare	(22)	T	- T	277	1	6 ^{35.3}		-	
Phyteuma tetramerum Aconitum anthora				(777)			15	20.0	
Arenaria serpyllifolia agg.			1		1	1 **		49.4	
Aconitum moldavicum Pedicularis exaltata	~				1		10 12	20.1	
Euphorbia illirica				0.0	6 (8) (6			11	31.6
Abundant bryophytes (EO) Rhytidiadelphus squarrosus		777	35753	1959	1	- 1	9 33.3	4	1112
Climacium dendroides Brachythecium mildeanum	2 7	5753	8	1	3 1	Charles and the same of the same of	9 44.0	4	
Plagiomnium cuspidatum				1	1 1	4	Ť		
Abietinella abietina Hypnum lindbergii			2	10	1	1 40.0	1		
Plagiomnium undulatum			1	1	1	1	0 **.*		
Calliergonella cuspidata Pleurozium schreberi	2	-	7	3	4	3 1	3 2	4	
Plagiomnium affine agg.	4		6	8 :	10 1		4	4	
Brachythecium albicans			1		7	-			
V									

Table 3: Phytosociological relevés of *Violo declinatae-Agrostietum capillaris* ass. nova. Nomenclatural type: relevé nr.20 is on a grey background. 1 – variant typicum (1-30), 2 – variant with *Cirsium erisithales* (31-40). *Dianthus barbatus* subsp. *compactus* – *Dianthus *compactus*, *Ranunculus polyanthemos* subsp. *nemorosus* – *Ranunculus *nemorosus*.

Variant	1 2
Relevé number	111111111112222222223 3333333334
CONTRACTOR	123456789012345678901234567890 1234567890
Violo declinatae-Agrostietum cap	
Angelica sylvestris	+allrl+a.+.l++++#111++a ++.r.r
Lotus ucrainious	.1+1.11.a111+1++11.++.+ +rrr
Trifolium alpestre	+11.ar1+1+1aaaaaaa+a.a a
Stachys officinalis	++.++r+1aa+++a11++1 a
Hieracium umbellatum	+1x1+1.+++++++ ++x
Trifolium pannonicum	.+r.+.+1+++11aa1++
Galium verum agg.	.+rl.a++++1111111
Stachys alpina	r
Cyanus mollis	+.1+
Achilles carpatics	
Viola declinata	rz
variant typicum	11++++x11a11.111a+10++1+4
Phleum pratense Leucanthemum vulgare agg.	+1++1+ra111+a1a11+1++a.+++r. +.+
Centaures jaces	+1.r1a3aaa1a11aaa1a
Anthoxanthum odoratum agg.	1.a.a1++131a1a++.a++.+.
Schedonorus pratensis	.1aa1ar.a.+111a3+.11a.+
variant with Cirsium erisithales	
Cirsium erisithales	41a.ar444
Lesexpitium letifolium	
Contaures kotschyans	
Aconitum anthora	
Festuca carpatica	
Polygono-Trisetion	AND AND STREET, AND STREET, AND
Astrentia major	++11aa11+a++a11+111a1a++11a a11a2aaaaa
Trollius europaeus	+11+aa111++++++11a111111.1+11aa .1+1.a1+++
Campanula serrata	+++r+.11++++++1++++1+ +++1+r1rr+
Alchemilla spec. div. Pimpinella major	a+1r1+1a111.+++a ar
Gerenium sylvaticum	+.+.+r++1+++.1a.++1.
Knautia dipsacifolia = maxima	+
Contaures phrygis agg.	1a1+a+.+ r.+a
Phytouma tetramerum	
Molino-Arrhenatheretea	
Lathyrus pratensis	.11ar.+a++++.+++.+++.++r+-r+.r.rrr.
Rhinanthus minor	1+3+aa+111.+1a1++++
Plantago lanceolata	+r.+1++1++.++1+
Myosotis scorpioides agg.	.++. <u>.</u> r.++.+++ ++ +++
Trifolium repens	+r1+a+++
Prunella vulgaris	r.1+1++++ +rrr
Cynosurus cristatus	+r1.+1111+3
Rumex acetosa Filipendula ulmaria	+.1+.+++
Trifolium pratense	rrrr r.a.a1/11b+.1 rr
Carum carvi	.+
Holous lanatus	3 1 1114
Succisa pratensis	+
Ranunculus acris	r.+++
Cirsium oleraceum	.+11
Festuco-Brometea	Contraction of the property of the contract
Campanula glomerata agg.	.+.++rr.+.+1++++++++++++++ +1+rrr.rrr
Ranunculus polyanthemos	/.+.+.r.,+++1+++++1+r. r.r
Pimpinella saxifraga agg.	+/x.+1+.+++.+++
Linum catherticum	r.+++++
Plantago media	.+1 +++
Anthyllis vulneraria	1+.a
Tragopogon pratensis agg.	1++
Trifolium montanum	+.+11

Medicago lupulina	
Mardetes strictse	
Potentilla erecta	++ls=lll.l++l+l+++l ls
Carex pallescens	.+++.1111+ +
Luzula luzuloidza	+ala
Luxula compostria agg.	l.++m++
Hypochecris uniflore	······································
Viole danine	+==++++
Polygala vulgaris Poa chaixii	3r 11
Potentilla aurea	F1000000000000000000000000000000000000
Mulgedio-Acomitetes	
Rumex arifolius	-++
Calamagrostis arundinacca	
Corestium fontenum agg.	
Silene divica	(ee. +
Delphinium eletum	
Calamagrostis villosa	
Checrophyllum hirautum	
Other species	and the contract of the contr
Agrostis capillaris	41415aa443443a13.a4aaa3a111a. +ra+a
Mcreeleum aphondylium	+11+.ss++.+++++++.+1+.111 +++s.ss=2s
Dectylia glomerata agg.	+11+++=+1.+11=11.+++.153.3. 1++=
Cruciate glabre	+.+++=:.+1.+++++.+.+.+.+.+.+.+
Achilles millefolium agg.	
Tenecctum corymbosum Stellerie gramines	.+++=1.+++al+llllal al=+= ++++.==++1!++1++++++++ ==
Hypericum maculatum	.+ll+a+++++++++1l+ + a+aa+
Thymus gulegioides	++.l1-l1+all1 TilaTagT
Brira media	+++,1++131+1,11,++,111,11,,1
Festuca subsa agg.	.a+a. 3.a11111aaa44+. ra
Carlina acaulis	+++111++ 1====
Cregis biennis	.1+1=1+.+.++++.+++11+
Gymnadenia conopsea	†==++. ++++++++++++++++++++++++++
Veronice chamaedrys agg.	+ss.tl.tt.tttt ss
Leontodon hispidus	.+==1b+1+.+1.+++++
Dianthus *compactus	
Trisctum flavescens	+1a.a.+4.aa341
Campanula patula	†† ******************************
Vicia crecca agg.	.+1+2++.++
Eughresie rostkoviene agg.	
Pos nomoralis	
Crepis conyzifolia	***************************************
Primula clation	
Deschangsia cospitosa	11:a 1.+1
Origanum vulgare	++.(1+2
Knautia arvensis agg.	
Cuscuta curopaca	
Helietochloa planiculmis	1
Avenula gubescens	1
Traunsteinera globosa	
Clinopodium vulgare	++++++
Lurula sudotica	+++
Renundulus lenuginosus	++
Fragaria vesca	
Euphrasia stricta 299.	······-
Pediculario exeltata Neottia ovata	.1+
	······································
Viola hirta Parnassia palustris	++++
Thelictrum equilogiifolium	
Euphorbia carniolica	
Vicia sylvatica	
Scabiosa lucida	
Dienthus superbus	
Polygonatum verticillatum	
	~ X / Y
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Scabiosa columbaria	
Lotus corniculatus agg.	+r
Aconitum moldavicum	r. 1r. 1
Ononis arvensis	
Lilium martagon	
Ajuga reptans	r
Pteridium aquilinum	5a1
Carex sempervirens	
Elvmus caninus	a. .1a
Melampyrum saxosum	
Helictochloa praeusta	a1+.
Digitalis grandiflora	
Crepis paludosa	
Carex umbrosa	
Ranunculus *nemorosus	1
Taraxacum sect. Ruderalia	r.++
Pilosella aurantiaca	r+
	+ + + + + + + + + + + + + + + + + + + +
Polygala comosa	
Silene vulgaris	+.r
Silene nutans	
Thesium alpinum	ra.r
Poa pratensis agg.	33
Holcus mollis	a.a
Carex montana	
Chaerophyllum aromaticum	a. a. a.
Elytrigia repens	
Trifolium medium agg.	11
Mercurialis perennis	
Cyanus montanus	
Carex sylvatica	
Danthonia decumbens	a+
Trifolium hybridum	++
Bunias orientalis	
Ranunculus breyninus	
Urtica dioica	+r. r.
Hypericum perforatum	+.r
Pilosella cymosa	r+
Geranium pratense	+r
Geranium phaeum	r
Arnica montana	1r
Rhinanthus alectorolophus agg.	r
Silene nemoralis	rr.
Aposeris foetida	rr.
Acer pseudoplatanus	
Picea abies	rrr
TIOUR GETTES	

Species occurring in less than four relevés

E₁: Acinos alpinus 36: r; Alopecurus pratensis 2: 1; Arabidopsis halleri 32: +; Aquilegia species 31: a; Bistorta officinalis 23: +; Bromus hordeaceus 10: 1; Calamagrostis epigejos 25: 1; Campanula persicifolia 26: +; Carduus kerneri 35: +; Carex flava agg. 2: +; Cirsium arvense 2: +; C. palustre 29: +; C. rivulare 2: +; Colchicum autumnale 27: +; Cuscuta species 7: r; Dactylorhiza maculata 12: +; D. majalis 23: +; Daucus carota 13: +; Dianthus carthusianorum agg. 6: r; D. deltoides 21: +; Dryopteris filix-mas 33: +; Epilobium angustifolium 4: +; Equisetum pratense 30: 1; E. sylvaticum 24: +; Festuca ovina agg. 1: +; F. stricta subsp. saxatilis 37: 3; Galeopsis tetrahit 10: 1; Gentiana asclepiadea 1: +; G. cruciata 6: r; Gentianella amarella 24: +; Geum rivale 33: +; Gladiolus imbricatus 16: 1; Glechoma hederacea agg. 33: +; Heracleum carpaticum 35: +; Hypericum hirsutum 18: +; Leontodon autumnalis 6: 1; Luzula sylvatica 26: +; Lysimachia vulgaris 26: +; Molinia caerulea 10: +; Myosotis arvensis 1: +; M. ramosissima 7: r; Myosoton aquaticum 29: r; Nardus stricta 1: +; Neotinea ustulata 14: +; Ononis spinosa 1: +; Pedicularis hacquetii 21: 1; Phleum alpinum 37: r; Phyteuma orbiculare 37: r; Polystichum aculeatum 32: +; P. lonchitis 32: +; Pulmonaria mollis 25: +; Rubus idaeus 4: +; Scorzoneroides autumnalis 1: +; Senecio nemorensis agg. 29: +; Silene flos-cuculi 2: +; Sisyrinchium montanum 1: +; Solidago virgaurea 25: +; Spiraea chamaedrifolia 25: +; Stachys sylvatica 6: r; Stellaria nemorum 26: +; Thymus alpestris 37: 1; Vaccinium vitis-idaea 1: +; Verbascum lanatum 35: r; Veronica urticifolia 25: +; Vicia sepium 40: r; *Viola arvensis* 13: +; *V. tricolor* 1: +. $-E_0$: *Pleurozium schreberi* 1: a.

Table 4: Ecological characteristics of associations.

Name of association	Slope	orientation	elevation m a.s.l.	soils	locality
Campanulo glomeratae-Geranietum sylvatici	2 –65°	various	630–1200	semi-deep to deep soils with varying limestone skeleton content	Starohorské vrchy Mts and south- eastern part of the Veľká Fatra Mts, Wolosate, Chyvchyny Mts
Geranio sylvatici-Trisetetum flavescentis	35(45)°	various	730–1200	mineral rich, moist and deep brown soils	Spišská Magura Mts, Belianske Tatry Mts, Tatry Zachodnie Mts and Pogórze Spisko-Gubałowskie Hills
Crepido mollis-Agrostietum capillaris	2 –36°	mostly northern	650–1400	moderately deep, clay to loamy-clay soils	Slovakia and Poland
Geranio-Alchemilletum crinitae	5–45°	various	750–1670	shallow to moderately deep, well aerated rendzina and pararendzina	Veľká Fatra Mts, Malá Fatra Mts, Belianske Tatry Mts, Tatry Zachodnie Mts
Alchemillo-Deschampsietum caespitosae	up to 35°	various	1100–1600	medium heavy to heavy, medium deep to deep, freshly wet, loamy- clayey, neutral to weakly alkaline soils (rendzina)	Slovakia, Poland, Romania, Ukraine
Phyteumo (orbicularis)-Trifolietum pratensis	2–25°	various	800–1360	shallow, well drained, rocky soils	Polish Tatra Mts, Slovenský raj Mt., Veľká Fatra Mts, Muránska planina Mts and rarely Nízke Tatry Mts, Chočské vrchy Mts and Malá Fatra Mts
Astrantio-Trisetetum flavescentis	2-20(30)°	various	800-1100	rendzinas or brown soils	entire study area
Violo declinatae-Agrostietum capillaris ass. nova	5–45°	various	800–1600	sod-brown soils with varying depth, brown mountain meadow soils of "polonynas" grasslands on the artificially deforested mountain ridges and the brown-grey soils in post-forest areas lower altitudes (800–1300 m a.s.l.) - slightly acidic to acidic soil reaction (pH 5.3–5.7) and low content of exchange bases mainly on the western and north-eastern slopes higher altitudes (1050–1600 m a.s.l.) - carbonate substrates on the dry north-eastern and eastern slopes with poorly developed, well-drained neutral or weakly alkaline soils with significant humus content in the upper horizon	Skybovy and Verkhovynsky Carpathians, Chyvchyny Mts
Trollio altissimi-Knautietum dipsacifoliae	5–25°	mostly sout-west	810–1450	Eutric-Gleyic Cambisols and Eutric Gleysols	Bieszczady Mts

Table 5: Correlation coefficients between the first two axes and environmental variables. Significant corelation coefficients are in bold.

	Correlations (DCA_score_env_factors) Marked correlations are significant at p < .00416 N=612 (Casewise deletion of missing data)												
Variable	species NR	AMT	TAR	AP	Altitude	Light	Temperature	Moisture	Soil Reaction	Nutrients			
DCA1	6491	5753	5527	.5957	.6591	4061	1670	.3489	.2097	.1355			
	p=0.00	p=0.00	p=0.00	p=0.00	p=0.00	p=0.00	p=.000	p=.000	p=.000	p=.001			
DCA2	.2047	.1867	.2018	1268	0569	.0311	.2216	3182	2847	4161			
	p=.000	p=.000	p=.000	p=.002	p=.160	p=.443	p=.000	p=.000	p=.000	p=0.00			



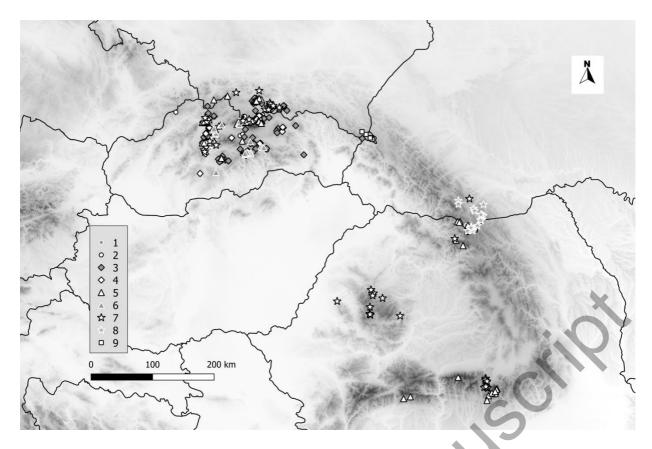


Figure 1. Distribution map of the *Triseto flavescentis-Polygonion bistortae* alliance in the Carpathians. 1 – Campanulo glomeratae-Geranietum sylvatici, 2 – Geranio sylvatici-Trisetetum flavescentis, 3 – Crepido mollis-Agrostietum capillaris, 4 – Geranio-Alchemilletum crinitae, 5 – Alchemillo-Deschampsietum caespitosae, 6 – Phyteumo (orbicularis)-Trifolietum pratensis, 7 – Astrantio-Trisetetum flavescentis, 8 – Violo declinatae-Agrostietum capillaris ass. nova, 9 – Trollio altissimi-Knautietum dipsacifoliae.

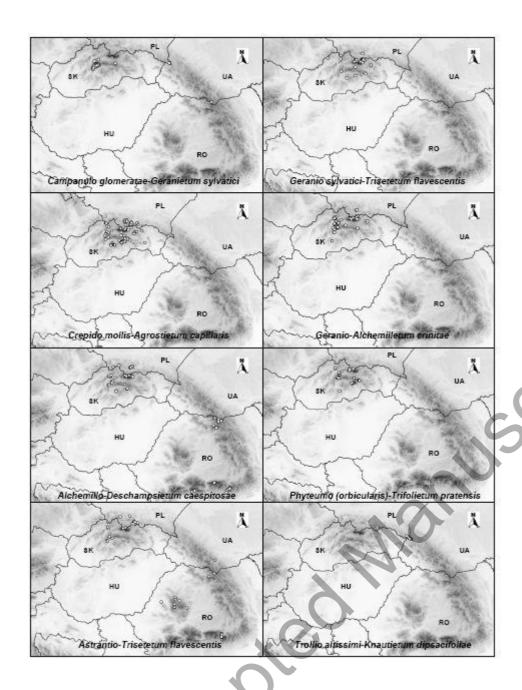


Figure 2. Distribution of clusters 1–7 and 9 in the study area.

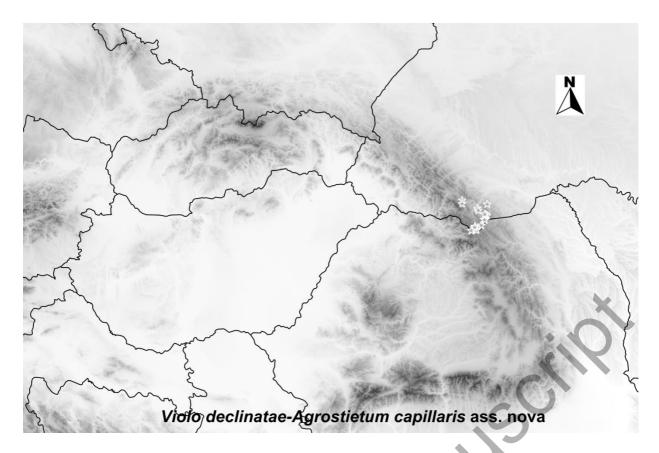


Figure 3. Distribution of Violo declinatae-Agrostietum capillaris ass. nova in the study area.

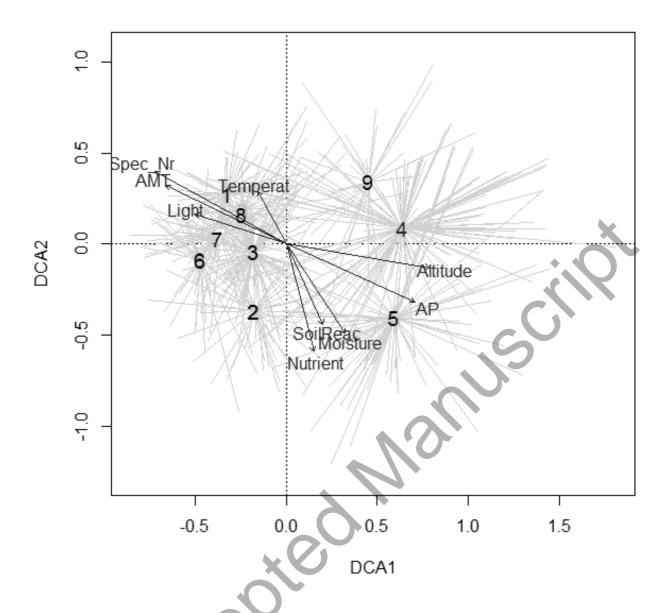


Figure 4. The DCA ordination diagram based on logarithmic transformed data of the Carpathians mountain hay meadows (length of gradient 2.9903; eigenvalues of the first two axes are 0.2731 and 0.1708). Selected indicator values for relevés (temperature, moisture, light, soil reaction and nutrients), altitude, climatic variables (annual precipitation – AP, annual mean temperature – AMT) and the number of vascular plant species for the relevés of individual clusters 1–9 were used as supplementary variables. 1 – Campanulo glomeratae-Geranietum sylvatici, 2 – Geranio sylvatici-Trisetetum flavescentis, 3 – Crepido mollis-Agrostietum capillaris, 4 – Geranio-Alchemilletum crinitae, 5 – Alchemillo-Deschampsietum caespitosae, 6 – Phyteumo (orbicularis)-Trifolietum pratensis, 7 – Astrantio-Trisetetum flavescentis, 8 – Violo declinatae-Agrostietum capillaris ass. nova, 9 – Trollio altissimi-Knautietum dipsacifoliae.

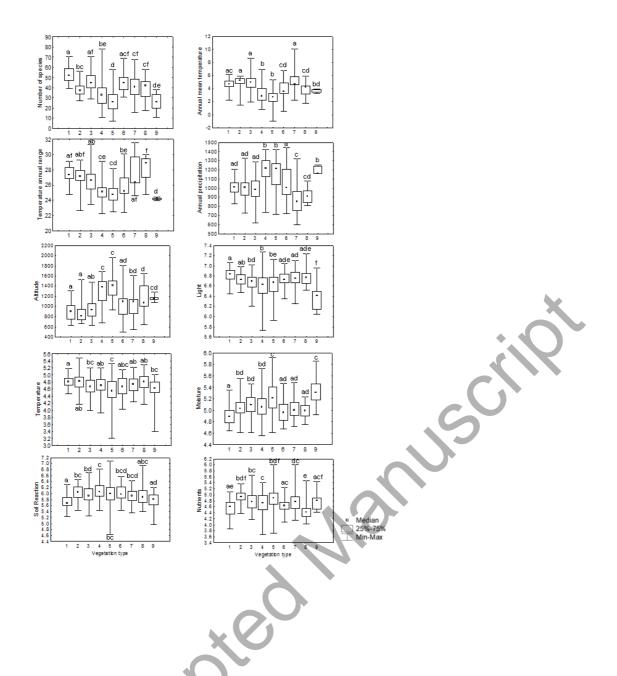


Figure 5. Box and Whisker plots of selected indicator values for relevés (temperature, moisture, light, soil reaction and nutrients), altitude, climatic variables (annual precipitation – AP, annual mean temperature – AMT) and number of vascular plant species for relevés in individual clusters 1–9. The boxes show medians and upper and lower quartiles and the whiskers indicate minimum and maximum values. Significant differences between clusters (Kruskal-Wallis ANOVA and multiple comparison tests of the mean ranks, P < 0.05) are marked by labels (a-f). The same letters indicate associations that did not differ significantly in a specifc parameter. 1 – Campanulo glomeratae-Geranietum sylvatici, 2 – Geranio sylvatici-Trisetetum flavescentis, 3 – Crepido mollis-Agrostietum capillaris, 4 – Geranio-Alchemilletum crinitae, 5 – Alchemillo-Deschampsietum caespitosae, 6 – Phyteumo (orbicularis)-Trifolietum pratensis, 7 – Astrantio-Trisetetum flavescentis, 8 – Violo declinatae-Agrostietum capillaris ass. nova, 9 – Trollio altissimi-Knautietum dipsacifoliae.