Formalized classification of semi-dry grasslands in central and eastern Europe

Formalizovaná klasifikace širokolistých suchých trávníků střední a východní Evropy

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European semi-dry grasslands are among the most species-rich vegetation types in the northern hemisphere and form an important part of the habitat mosaics in the forest-steppe zone. However, there is no comprehensive evaluation of the variation in their composition and the phytosociological classification of these grasslands. For the syntaxonomic revision, we used a dataset of 34,173 vegetation plot records (relevés) from central and eastern Europe, which were assigned to the class *Festuco-Brometea* using the diagnostic species listed in the EuroVegChecklist. To determine the diagnostic species of the orders, we used a TWINSPAN classification of the whole dataset. Of the total dataset, 15,449 relevés were assigned to the order *Brachypodietalia pinnati*, which corresponds to semi-dry grasslands. This subset was again classified using TWINSPAN. Formal definitions of the following alliances were established: *Mesobromion erecti*, *Cirsio-Brachypodion pinnati* (incl. *Fragario-Trifolion montani*, *Agrostio-Avenulion schellianae*, *Scabioso ochroleucae-Poion angustifoliae* and *Adonido vernalis-Stipion tirsae*), *Scorzonerion villosae* and *Chrysopogono-Danthonion.* Another alliance, *Armerion elongatae* (= *Koelerio-Phleion phleoidis* p.p.), is transitional towards the class *Koelerio-Corynephoretea* and its status needs further evaluation. We also established formal definitions of all of the associations of *Mesobromion* and *Cirsio-Brachypodion* within the area studied. Associations were identified using (i) a TWINSPAN classification of the whole order, (ii) TWINSPAN classifications of regionally restricted data sets (usually all *Brachypodietalia* plots in one country) and (iii) existing national classification schemes. All formal definitions were written in the expert system language of the JUICE program. To obtain a more complete picture of the floristic similarities and gradients, we performed a DCA ordination of the associations. Our results revealed that meadow steppes in the forest-steppe zone in eastern Europe are very similar to semi-dry grasslands in central Europe.

Keywords: *Brachypodietalia pinnati*, *Cirsio-Brachypodion*, *Festuco-Brometea*, meadow steppe, *Mesobromion*, semi-dry grassland, syntaxonomy, vegetation classification

Introduction

Semi-dry grasslands in Europe are among the most species-rich communities in the world (Wilson et al. 2012, Roleček et al. 2014, Chytrý et al. 2015). However, the area of these grasslands has strongly declined during the last century, and the remaining sites are endangered due to changes in management practices and atmospheric nitrogen deposition (Veen et al. 2009, Janssen et al. 2016, Hülber et al. 2017). In central Europe, semi-dry grasslands are usually considered as man-made habitats, which were created by grazing or mowing after clearing of the original forest (Poschlod & WallisDeVries 2002). The meadow steppes in eastern Europe, by contrast, were thought to be naturally treeless ecosystems (Walter 1974). However, recent studies show that both assumptions are too simplistic and do not reflect the complex history and ecology of European semi-dry grasslands. On the one hand, there is increasing evidence that at least some central European grasslands developed directly from the hemiboreal forest-steppe of the early Holocene (Magyari et al. 2010, Kuneš et al. 2015, Pokorný et al. 2015). On the other hand, long-term observations in strictly protected steppe reserves in the forest-steppe zone in eastern Europe demonstrate that most meadow steppes are dependent on natural or human disturbances such as fire, grazing or mowing (Filatova et al. 2014).

The term "meadow steppe" has been used with varying meanings in the literature. Here we define meadow steppes as semi-dry grasslands with a large proportion of steppe species with a Siberian-Pontic-Pannonian distribution. In this sense, the semi-dry grasslands in eastern and east-central Europe are meadow steppes, while those in western and west-central Europe are not.

The phytosociological classification of the European dry and semi-dry grasslands (class *Festuco-Brometea*) was originally developed with the main focus on the driest types, which are profoundly different in the western and eastern part of Europe (Braun-Blanquet 1936, Klika 1939). The semi-dry grasslands were only considered as mesic subtypes of these biogeographical units, which initially were distinguished at the level of alliances (*Bromion erecti* versus *Festucion valesiacae*), and later at the level of orders (*Brometalia erecti* versus *Festucetalia valesiacae*) (Braun-Blanquet & Tüxen 1943, Klika & Hadač 1944). The semi-dry grasslands in west-central Europe were included in the alliance *Mesobromion*, and the meadow steppes in east-central Europe in *Cirsio-Brachypodion*, although the exact delimitation of these two units remained unclear (Illyés et al. 2007). Krausch (1961) was probably the first author who raised doubts about this syntaxonomic concept. He proposed to unite *Mesobromion* and *Cirsio-Brachypodion* within a separate order of semi-dry grasslands, pointing to the fact that most of the character species listed for *Brometalia erecti* in the original sense are absent in *Mesobromion*, while the latter has many species in common with *Cirsio-Brachypodion*. He also suggests that *Cirsio-Brachypodion* should be extended to eastern Europe because of the close floristic relationship between the meadow steppes in eastern and central Europe.

The idea of a common order of semi-dry grasslands was adopted by Korneck (1974), who introduced the name *Brachypodietalia pinnati* for this unit, but the concept of geographical orders remained dominant for the next two decades (Royer 1991, Dierschke 1997). Further alliances of semi-dry grasslands were described from the Balkan Peninsula, in particular *Scorzonerion villosae* and *Chrysopogono-Danthonion alpinae* (Horvat et al. 1974). In the most recent overview of European high-rank syntaxa (Mucina et al. 2016), the order *Brachypodietalia pinnati* was accepted, but *Scorzonerion villosae* was not included in this order, and the syntaxonomic position of the eastern European meadow steppes is unclear (see also Kuzemko et al. 2014, Willner et al. 2017b). According to the International Code of Phytosociological Nomenclature (Weber et al. 2000), the name *Brometalia erecti* has priority over *Brachypodietalia pinnati* and *Bromion erecti* has priority over *Mesobromion*. However, both younger synonyms have been proposed as nomina conservanda (Dengler et al. 2003, Theurillat et al. 2017). Considering these proposals as well justified, and for the convenience of the reader, we use these nomina conservanda proposita throughout the paper, although there are no formal decisions on these proposals.

In this study, we present a syntaxonomic revision of the semi-dry grasslands in central and eastern Europe. Specifically, we aim to (i) identify the main compositional gradients using numerical classification and ordination methods, and (ii) establish formal definitions of the orders, alliances and associations, which enable unambiguous assignment of new plot records to the accepted vegetation units.

Materials and methods

Area studied

The area studied comprises central and eastern Europe as well as the northern half of south-eastern Europe (Fig. 1). Thus, it stretches from the Rhine river in the west to the Urals mountains in the east, and from the central Balkans in the south to the Baltic Sea in the north. We included data from the following countries (from west to east): Germany, Austria, Czech Republic, Poland, Slovakia, Hungary, Slovenia, Croatia, Serbia, Romania, Bulgaria, Ukraine and Russia.

Data set

Most data were obtained from large vegetation-plot databases (e.g. Chytrý & Rafajová 2003, Aćić et al. 2012, Dengler & Rūsiņa 2012, Jandt & Bruelheide 2012, Jansen et al. 2012, Kuzemko 2012, Vassilev et al. 2018), accessed via the European Vegetation Archive (EVA; Chytrý et al. 2016). A smaller amount of data was directly provided by co-authors or computerized from literature (see Electronic Appendix 1 for a complete list of the sources). We selected all relevés in which (i) the diagnostic species of the class *Festuco-Brometea* according to Mucina et al. (2016) had a higher total percentage cover than the diagnostic species of any other class and, at the same time, (ii) the total cover of *Festuco-Brometea* species was at least 10% and (iii) at least four *Festuco-Brometea* species were present. The total percentage cover was calculated according to Fischer (2015). Using the sum of square-rooted percentage cover instead of total cover resulted in very similar results. However, the total percentage cover was mostly in better accordance with the original classification of the relevés, and therefore we used it in this and in all the following steps.

The taxonomy and nomenclature of vascular plants were checked and harmonized following the Euro+Med PlantBase (www.emplantbase.org; accessed February 2018). Lichens and bryophytes were not considered in our analysis as they were only recorded in a subset of the relevés. Species with inconsistent or frequently doubtful determination were merged into aggregates (Electronic Appendix 2). Taxa determined only at the genus level were excluded except when there was no other taxon of the same genus in the dataset. Relevés in which the taxa determined only at the genus level had a total cover > 6% were removed from the dataset. We also excluded relevés with a total cover of trees and shrubs > 25% and relevés with a plot size < 9 m^2 or > 100 m^2. However, relevés without plot size information were not excluded as they were too many and we expected that the vast majority of them fell within the allowed range (like 88% of the plots with plot size information). This resulted in a dataset of 34,173 plot records.

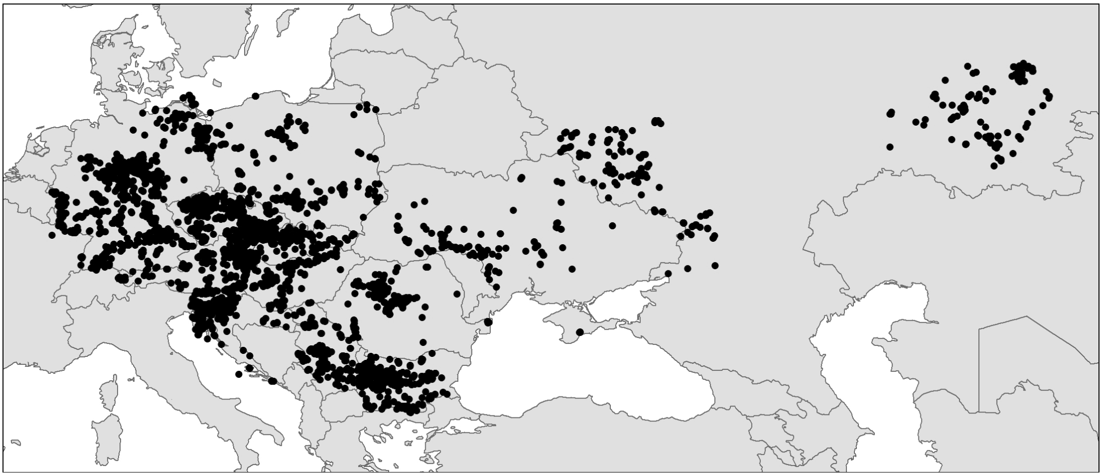

Fig. 1. – Map showing the areas studied and the geographical distribution of the plots assigned to the target order *Brachypodietalia pinnati* (black dots).

Classification step 1: phytosociological orders

For classifying the relevés into phytosociological orders, we mainly relied on the diagnostic species identified by Willner et al. (2017b). However, as our new dataset covered a considerably larger geographical area than the previous study, we also did a TWINSPAN classification of the whole dataset (see Electronic Appendix 3 for details). Most of the previously established diagnostic species for the orders *Brachypodietalia pinnati*, *Festucetalia valesiacae* and *Stipo-Festucetalia pallentis* were reproduced, while some species not considered as diagnostic in the previous paper, mostly because they had a very low constancy in the old dataset, were added to the diagnostic species lists (Electronic Appendix 3). Based on these revised lists of diagnostic species, we assigned all relevés to one of the above three orders using the same approach as for the classes (i.e. each relevé was assigned to the order with the highest cover score). 16,198 relevés were assigned to our target order *Brachypodietalia pinnati*. However, during the following steps, we realized that some of them were clearly misclassified and did not belong to the target order (mostly not even to the class *Festuco-Brometea*). Therefore, only 15,449 relevés were used in the final analysis.

Classification step 2: alliances

We classified the *Brachypodietalia* dataset with TWINSPAN using WinTWINS 2.3 (Hill & Šmilauer 2005). Cut levels of pseudospecies were set to 0, 5 and 25% cover, respectively. Species with less than five occurences were excluded. The maximum number of division levels was six and the minimum group size for division was two. To test for the influence of different sampling densities in different parts of the area studied, we also classified a dataset where only a random selection from the two countries with the highest number of plots (Germany and the Czech Republic) was included. Since the overall patterns in the two classifications were very similar (data not shown) we used the one with all plots included. Based on the interpretation of this unsupervised classification, we established formal definitions for the alliances based on diagnostic species (see below for the general structure of these definitions) and reassigned all relevés using the expert system functions in the JUICE program (see Appendix S2 in Landucci et al. 2015).

Classification step 3: associations

We classified the relevés of two alliances (*Mesobromion*, *Cirsio-Brachypodion*) to the association level. The other alliances were not further analysed as their occurrence was marginal with respect to the area studied or their syntaxonomic position was transitional towards another class. We followed the association concept of Willner (2006), who defined the association as "the smallest syntaxonomic unit having an unambiguously defined floristic as well as ecological or biogeographical content". While the first part of the definition (the defined floristic content) can be satisfied by establishing formal definitions, the second part is more hypothetical – it means that one should be able, at least in theory, to predict an association from environmental data, site history and geographical location. Therefore, associations could be seen as falsifiable and mutually exclusive hypotheses based on a correlation between species composition (as a response variable) and external factors (as predictors). However, since we did not have measurements of the environmental conditions, we mainly relied on expert judgement, while testing the accepted associations for ecological differences (e.g. soil parameters, management regime) remain to be studied in the future.

The delimitation of the associations was done in a multistage supervised process. First, we grouped all relevés of a given alliance by countries. Then we classified the relevés of each alliance and country into preliminary associations, taking into account (i) the TWINSPAN classification of the *Brachypodietalia* dataset, (ii) additional TWINSPAN classifications of geographically restricted datasets (usually all relevés from one country), and (iii) national vegetation surveys and other phytosociological literature. In this way, we tried to identify units that were reproducible by unsupervised numerical classification methods both in a regional and supra-regional context and that, as much as possible, corresponded to units already recognized in previous studies. The resulting "operational units" were rearranged in such a way that units corresponding to the same or closely related associations were adjacent to each other. This table was used as a template for creating formal definitions. Finally, the expert system was used to reassign all relevés of the two target alliances to the defined associations.

Formal definitions of alliances and associations

In comparison with the class and order level, the formal definitions of the alliances and associations are more complex and reflect the often reticulate floristic relationships between syntaxa of lower ranks. Thus, instead of using a single diagnostic species list for each unit, the definitions are based on a larger set of species groups, which are not mutually exclusive (i.e. one species can be a member of more than one group). Three principal kinds of membership conditions are used: (i) presence or absence of a species group, (ii) presence or absence of a single species (equivalent to a species group with only one member) and (iii) comparison of the total cover of two species groups. A species group is considered as present when at least one of its members occurs. In some cases, threshold cover values are used, which means that a species or a species group is only considered as diagnostic if its total cover exceeds a certain value.

Potential diagnostic species were determined using the phi coefficient of association (Chytrý et al. 2002, Tichý & Chytrý 2006), constancy ratio (Dengler 2003) and cover ratio (Willner et al. 2009). The criteria for diagnostic species were basically the same as in Willner et al. (2017b). However, after some trials it became clear that, in particular for geographically vicariant units, not all species formally meeting the criteria for diagnostic species could be used in the expert system, because they created a lot of misclassified relevés. Moreover, in some cases the inclusion of species with lower fidelity considerably improved the performance. Thus, the main selection criterion for diagnostic species was their suitability for sharply discriminating the vegetation units along the chosen gradient, i.e. the ecological or geographical gradient that should be reflected in the classification.

Stratification and ordination

The result of reassigning all relevés to associations is presented in a constancy table. Since the constancy values might be biased due to varying sampling densities in different regions, we did a stratified random resampling within each association. A maximum of five relevés from each grid cell (12' latitude × 20' longitude) were selected. Relevés without coordinates (< 5% in 34 of 44 associations, > 20% in only five associations containing altogether only 137 relevés) were considered as one stratum. Alliances not classified into associations were stratified as a single association.

To get a more complete picture of the floristic similarities and gradients among the accepted associations, we also performed a DCA ordination using the percentage constancy values of species instead of abundances. Finally, we arranged the associations within each alliance into informal association groups to facilitate the interpretation of the results, but these groups were not fully formalized.

Environmental evaluation

The position of each association along environmental gradients such as soil pH and temperature was evaluated using Borhidi indicator values (Borhidi 1995). For each relevé of the stratified data set, we calculated the unweighted mean of species indicator values, which gives a rough approximation of the local site conditions. Of the total number of taxa 1,069 taxa (= 47%) did not have indicator values and therefore were not included in the calculation. However, apart from aggregates, only 21 of them had more than 100 occurrences in the data set (e.g. *Bromopsis riparia*, *Cirsium acaulon*, *Gentianella germanica* and *Thymus longicaulis*).

Results

Unsupervised classification

The TWINSPAN classification of the *Brachypodietalia* dataset revealed a predominant biogeographical pattern. The following main groups were detected (cluster numbers according to the 6th level of division, see Electronic Appendix 4): semi-dry grasslands in north-western central Europe (1–8), transitions to rocky grasslands and mesic *Sesleria*

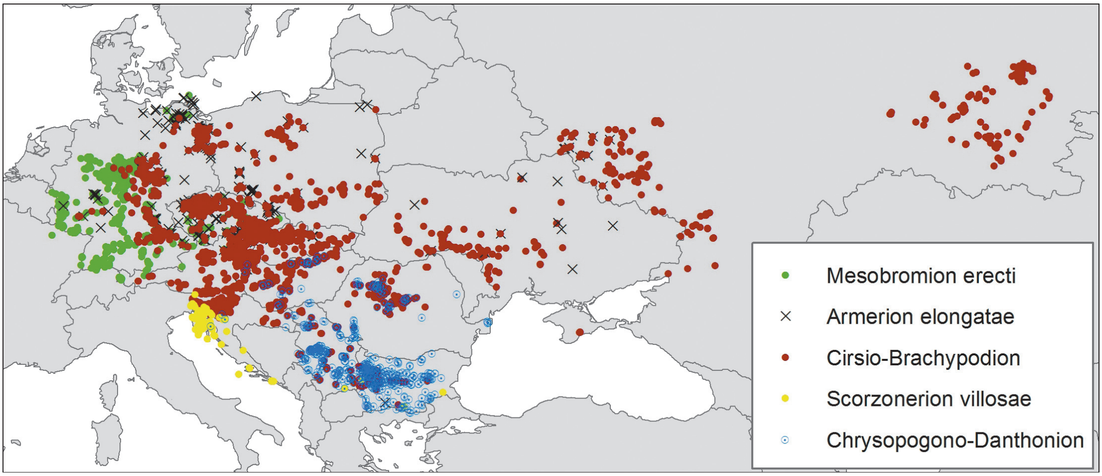

Fig. 2. – Geographical distribution of the plots assigned to the alliances *Mesobromion erecti*, *Armerion elongatae*, *Cirsio-Brachypodion*, *Scorzonerion villosae* and *Chrysopogono-Danthonion*.

caerulea grasslands in north-western central Europe (9–16), semi-dry grasslands in the German Jura Mountains, eastern Alps and NW Dinaric Mountains, with outliers in the Western Carpathians and Serbia (17–32), grasslands on sandy and siliceous soils, mostly in the northern part of central Europe (33–36), Pannonian meadow steppes on relatively mesic soils (37–38), Pannonian meadow steppes on dry soils, including most meadow steppes in Ukraine and some grasslands in NW Bulgaria (39–40), meadow steppes in European Russia (41–48) and semi-dry grasslands in SE Europe, mostly on acidic soils (49–64).

Alliances

We defined the following four geographically distinct alliances within the order *Brachypodietalia pinnati*: *Mesobromion erecti* (west-central Europe), *Cirsio-Brachypodion pinnati* (east-central and eastern Europe), *Scorzonerion villosae* (Adriatic region) and *Chrysopogono-Danthonion alpinae* (Balkan Peninsula) (Table 1, Fig. 2). *Mesobromion*, *Cirsio-Brachypodion* and *Chrysopogono-Danthonion* were strongly supported by the TWINSPAN classification (corresponding to clusters 1–16, 35–48 and 49–64, respectively). *Scorzonerion villosae*, in contrast, did not form a coherent group in the TWINSPAN table but it occurred interspersed within *Cirsio-Brachypodion* and *Chrysopogono-Danthonion* (mainly in clusters 37, 38, 52 and 56). However, as this pattern could be due to the relatively small number of relevés for this unit, we preliminarily accepted it as a separate alliance. For the reasons discussed below, we included the meadow steppes in European Russia (clusters 41–48) in *Cirsio-Brachypodion*, and split the peri-Alpine grasslands in clusters 17–32 between *Mesobromion* and *Cirsio-Brachypodion*. As a fifth alliance, we defined *Armerion elongatae* (= *Koelerio-Phleion phleoidis* p.p.), which mainly corresponds to clusters 33–34. Its geographical range overlaps those of *Mesobromion* and *Cirsio-Brachypodion*. However, including it in one of these alliances proved unsatisfactory as their diagnostic species are mostly absent.

Table 1. – Simplified visualization of the formal definitions of alliances and association groups. Shaded frames: diagnostic species of alliances. Non-shaded frames and frames within larger frames: diagnostic species of association groups. Open frames: diagnostic species differentiating only against the units to the left. Dashed frames: negative diagnostic species of alliances. Values are percentage constancies. Letters after the species names indicate putative character species of alliances. M: *Mesobromion*, A: *Armerion elongatae*, C: *Cirsio-Brachypodion*, S: *Scorzonerion villosae*, D: *Chrysopogono-Danthonion*.

Alliance	M	M	M	A	C	C	C	C	C	C	C	C	C	C	S	D
Association group	1	2	3		1	2	3	4	5	6	7	8	9	10		
Number of relevés	35	960	224	345	1385	920	195	28	79	7	190	93	162	36	102	577
Festuca ovina agg. (M)	100	80	92	53	3	4	3	.	.	.	.	.	.	.	13	.
Potentilla verna agg.	31	62	26	26	12	16	7	.	.	.	3	.	.	.	1	.
Gentianella germanica (M)	.	20	39	.	1	1	5	.	1	.	.	.	.	.	.	.
Ranunculus bulbosus	51	43	44	15	9	28	41	4	3	.	.	.	.	.	17	7
Bromopsis erecta	.	54	82	1	31	46	89	93	5	.	.	.	.	.	81	2
Carlina acaulis	.	18	44	12	12	27	46	7	4	.	.	.	.	.	13	3
Cirsium acaulon (M)	49	58	29	4	13	15	5	.	.	.	.	.	.	.	6	1
Polygala amara agg.	.	11	27	1	1	2	6	.	.	.	.	.	.	.	.	.
Carex flacca	26	52	70	1	6	29	67	.	.	.	.	.	.	.	37	.
Euphorbia verrucosa	.	4	26	.	1	2	38	.	.	.	.	.	.	.	22	.
Gentianella ciliata	.	20	25	.	2	4	5	.	.	.	.	.	.	.	1	.
Ophrys insectifera	.	6	13	.	1	1	2	.	.	.	.	.	.	.	.	.
Buphthalmum salicifolium	.	1	57	.	3	6	79	.	.	.	.	.	.	.	27	.
Rhinanthus glacialis	.	.	20	.	1	1	26	.	.	.	.	.	.	.	19	.
Armeria maritima (A)	.	.	.	16	1	1	.	.	.	.	1	.	.	.	.	1
Myosotis stricta	.	1	.	15	1	1	.	.	.	.	.	.	1	3	.	3
Jasione montana	.	.	.	12	1	1	.	.	.	.	.	.	.	.	.	1
Agrostis vinealis	.	1	.	17	1	1	1	.	.	.	1	3	6	.	.	1
Cerastium semidecandrum	6	1	.	14	1	1	.	.	.	.	2	.	.	.	.	2
Silene viscaria	.	1	.	27	1	2	1	.	.	.	3	8	8	11	.	6
Helichrysum arenarium	.	.	.	23	2	1	.	.	.	.	10	12	1	28	.	.
Artemisia campestris	.	1	.	34	16	3	.	.	.	.	21	45	8	39	2	1
Centaurea stoebe	.	1	.	26	24	8	2	11	25	.	11	29	4	33	.	15
Potentilla argentea	.	1	.	35	4	5	1	11	15	43	31	26	52	58	3	34
Rumex acetosella	3	1	.	30	3	4	.	4	6	.	6	3	7	14	4	20
Festuca stricta subsp. *trachyphylla* (A)	.	.	.	14	6	1	.	.	.	.	.	.	.	.	1	.
Festuca valesiaca agg.	.	.	.	26	71	80	76	50	28	100	69	88	77	75	51	59
Veronica spicata	.	.	.	26	19	8	1	.	.	.	9	37	40	50	3	6
Astragalus onobrychis	.	.	.	1	7	2	.	.	16	.	11	13	1	3	1	5
Euphorbia nicaeensis	.	.	.	.	5	.	.	.	1	.	8	1	1	25	6	2
Scabiosa ochroleuca	.	.	.	16	35	31	10	7	9	.	24	48	12	19	1	11
Potentilla incana agg.	.	.	.	14	35	9	1	.	38	.	14	5	3	.	3	3
Adonis vernalis (C)	.	.	.	1	16	3	1	.	1	86	5	34	51	3	.	4
Campanula sibirica	.	.	.	2	12	2	1	.	.	14	14	48	19	.	.	4
Inula ensifolia	.	.	.	1	14	2	2	.	6	43	.	10	6	.	1	2
Polygala major	.	.	.	.	10	5	4	50	23	43	.	.	.	.	.	11
Carex michelii (C)	.	.	.	.	10	5	5	.	.	.	.	11	17	3	.	1
Veratrum nigrum (C)	.	.	.	.	1	2	1	7	9	.	.	1	11	.	2	2
Pulmonaria mollis	.	.	.	.	1	3	.	.	.	.	.	.	1	.	.	1
Lathyrus pannonicus	.	.	.	.	1	3	3	.	.	57	.	1	13	8	.	1
Viola ambigua	.	.	.	.	4	1	.	.	.	.	5	16	6	17	.	1

Alliance	M	M	M	A	C	C	C	C	C	C	C	C	C	C	S	D
Association group	1	2	3		1	2	3	4	5	6	7	8	9	10		
Number of relevés	35	960	224	345	1385	920	195	28	79	7	190	93	162	36	102	577
Sesleria heuflerana	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.
Cirsium pannonicum (C)	.	.	.	.	5	10	53	.	.	.	.	.	1	.	15	2
Knautia drymeia	.	.	.	.	1	4	30	.	1	.	.	.	.	.	3	1
Stipa tirsa (C)	.	.	.	.	5	1	.	.	.	100	.	.	16	92	.	1
Phlomis tuberosa (C)	.	.	.	.	1	1	.	.	1	71	10	30	63	39	.	1
Elytrigia intermedia	.	.	.	1	14	5	1	.	3	.	18	29	23	22	3	6
Nonea pulla	.	.	.	1	3	2	.	.	3	.	16	38	24	19	.	3
Stipa pennata	.	.	.	.	7	2	.	.	3	.	.	74	70	86	1	1
Veronica prostrata	.	.	.	3	5	2	.	.	.	.	9	23	8	14	.	1
Stipa capillata	.	.	.	3	8	1	.	.	.	.	2	28	6	33	.	1
Pontechium maculatum (C)	.	.	.	.	2	2	.	.	3	.	1	14	4	22	.	3
Cytisus ruthenicus	.	.	.	1	1	.	.	.	.	.	10	41	43	50	.	.
Bromopsis riparia	.	.	.	.	.	.	.	4	24	.	1	25	21	53	.	1
Iris aphylla (C)	.	.	.	.	1	1	.	.	.	.	1	14	28	8	.	.
Salvia nutans	.	.	.	.	1	1	.	.	.	.	1	47	10	28	.	1
Arenaria procera (C)	.	.	.	1	1	1	.	.	.	.	1	25	17	17	.	1
Dracocephalum ruyschiana (C)	.	.	.	.	.	.	.	.	.	.	.	.	27	.	.	.
Euphorbia subtilis	.	.	.	.	.	.	.	.	.	.	.	12	20	11	.	.
Euphorbia semivillosa	.	.	.	.	.	.	.	.	.	.	1	1	24	.	.	.
Pedicularis kaufmannii	.	.	.	.	.	.	.	.	.	.	1	5	14	8	.	.
Helictochloa hookeri subsp. *schelliana*	.	.	.	.	1	.	.	.	.	.	.	6	21	.	.	.
Linum nervosum	.	.	.	.	1	1	.	.	.	.	.	3	7	8	.	1
Scorzonera villosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	42	.
Knautia illyrica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	48	.
Eryngium amethystinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	42	.
Koeleria lobata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	.
Leucanthemum platylepis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	28	.
Bupleurum gussonei	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	.
Ferulago campestris (S)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17	.
Helichrysum italicum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.
Carlina corymbosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.
Danthonia alpina (D)	.	.	.	.	2	3	19	18	4	.	.	.	.	.	22	52
Chrysopogon gryllus	.	.	.	.	2	1	.	.	1	.	.	.	.	.	41	62
Moenchia mantica (D)	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	20
Rhinanthus rumelicus (D)	.	.	.	.	1	2	.	21	4	.	.	.	.	.	.	32
Trifolium incarnatum	.	.	.	.	1	.	.	.	.	.	.	.	.	.	6	19
Trifolium strictum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Pilosella pavichii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
Dianthus cruentus	.	.	.	.	1	.	.	50	.	.	.	.	.	.	.	6
Dianthus giganteus	.	.	.	.	1	1	3	.	.	.	.	.	.	.	.	5
Silene sendtneri	.	.	.	.	.	.	.	50	5	.	.	.	.	.	.	5
Pedicularis heterodonta	.	.	.	.	1	.	.	46	.	.	.	.	.	.	.	3
Knautia dinarica	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	3
Campanula sparsa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Cynosurus echinatus	.	.	.	.	.	.	.	.	1	.	.	.	.	.	4	10
Plantago subulata	.	.	.	.	.	1	.	.	4	.	.	.	.	.	.	5
Helictochloa pratensis	43	29	35	28	16	16	1	.	.	.	.	.	.	.	.	6

Alliance	M	M	M	A	C	C	C	C	C	C	C	C	C	C	S	D
Association group	1	2	3		1	2	3	4	5	6	7	8	9	10		
Number of relevés	35	960	224	345	1385	920	195	28	79	7	190	93	162	36	102	577
Phleum phleoides	3	6	3	40	27	14	1	39	6	57	11	30	51	42	.	9
Brachypodium pinnatum agg.	.	79	79	8	66	62	72	11	42	.	.	1	13	.	46	19
Carex montana	.	14	49	.	4	15	44	18	1	.	2	1	8	.	6	2
Cruciata glabra	.	.	.	1	4	11	31	.	20	.	.	.	.	.	8	2
Thymus longicaulis	.	.	.	.	1	1	35	7	33	.	.	.	.	.	55	6
Koeleria pyramidata agg.	.	75	78	46	44	41	69	54	23	71	30	44	20	50	39	27
Salvia pratensis	.	25	46	19	54	50	69	4	1	.	45	58	28	11	64	16
Asperula cynanchica	.	30	50	17	45	29	31	39	37	.	20	30	8	6	17	25
Teucrium chamaedrys	.	14	21	4	44	26	50	21	77	86	38	.	.	3	25	38
Hippocrepis comosa	.	36	74	.	8	6	40	.	4	.	.	.	.	.	38	1
Onobrychis viciifolia	.	13	42	1	9	11	16	.	.	.	.	.	.	.	.	5
Phyteuma orbiculare	.	1	38	.	1	1	15	.	.	.	.	.	.	.	1	.
Polygala chamaebuxus	3	1	20	1	1	1	15	.	.	.	.	.	.	.	3	.
Crepis alpestris	.	.	15	.	1	.	3	.	.	.	.	.	.	.	.	.
Allium carinatum	.	1	11	.	1	2	21	.	8	.	.	.	.	.	6	1
Cerastium moesiacum	.	.	.	.	.	.	.	39	4	.	.	.	.	.	.	2
Ranunculus montanus	.	1	2	.	.	.	.	50	8	.	.	.	.	.	.	5
Gentiana utriculosa	.	.	.	.	.	.	3	64	.	.	.	.	.	.	3	2
Centaurea orientalis	.	.	.	.	1	.	.	21	5	.	1	.	.	3	.	2
Centaurea kotschyana	.	.	.	.	.	.	.	21	.	.	.	.	.	.	.	.
Seseli peucedanoides	.	.	.	.	1	1	.	21	22	.	.	.	.	.	.	1
Carlina acanthifolia	.	.	.	.	1	.	.	21	39	.	1	.	.	.	.	5
Festuca dalmatica agg.	.	.	.	1	.	.	.	.	48	.	.	.	.	.	2	6
Sesleria latifolia	.	.	.	.	.	.	.	.	38	.	.	.	.	.	.	.
Leontodon crispus	.	.	.	1	1	1	.	21	42	.	.	.	.	.	21	10
Asperula purpurea	.	.	.	.	1	.	1	14	25	.	.	.	.	.	3	1
Cerastium banaticum	.	.	.	1	.	1	.	14	34	.	.	.	.	.	1	1
Galium rhodopeum	.	.	.	1	.	.	.	.	10	.	.	.	.	.	.	1
Artemisia chamaemelifolia	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	1
Bromopsis cappadocica	.	.	.	.	.	.	.	.	.	86	.	.	.	.	.	.
Thymus roegneri	.	.	.	1	.	.	.	.	14	100	.	.	.	.	1	5
Cerastium biebersteinii	.	.	.	.	.	.	.	.	.	71	.	.	.	.	.	.
Cruciata taurica	.	.	.	.	.	.	.	.	.	29	.	.	.	.	.	.
Asperula tenella	.	.	.	.	.	.	.	.	.	14	.	.	.	.	1	1
Gypsophila altissima	.	.	.	.	.	.	.	.	.	.	.	34	14	3	.	.
Eryngium planum	.	.	.	2	2	1	.	.	.	.	11	30	9	6	.	1
Echinops ritro	.	.	.	.	.	.	.	.	.	.	.	23	2	3	2	.
Polygala sibirica	.	.	.	1	1	.	.	.	.	.	1	18	6	.	.	.
Galium octonarium	.	.	.	.	.	.	.	.	1	.	10	11	2	69	.	1
Verbascum marschallianum	.	.	.	.	.	.	.	.	.	.	2	4	3	61	.	.
Pilosella echioides	.	.	.	2	1	1	.	.	.	.	5	4	6	61	.	1
Stipa dasyphylla	.	.	.	.	1	.	.	.	.	.	.	.	6	50	.	.
Seseli tortuosum	.	.	.	.	.	.	.	.	.	.	6	2	.	42	.	1
Artemisia pontica	.	.	.	.	1	1	.	.	.	.	1	2	4	39	.	.

The expert system assigned 4,757 relevés to *Mesobromion*, 6,742 to *Cirsio-Brachypodion*, 214 to *Scorzonerion villosae*, 1,436 to *Chrysopogono-Danthonion* and 481 to *Armerion elongatae,* while 1,819 (= 12%) remained unclassified. The formal definitions of the alliances are given in Electronic Appendix 5.

Associations

We defined seven associations within *Mesobromion* and 37 within *Cirsio-Brachypodion*. Seven relevés of *Mesobromion* (= 0.1%) and 741 relevés of *Cirsio-Brachypodion* (= 11%) remained unclassified. To provide a better picture of the internal floristic and biogeographical structure of the alliances, we arranged the associations into informal association groups (Table 1). For a full synoptic table showing all the associations see Electronic Appendix 6; for more detailed descriptions and distribution maps of all the associations see Electronic Appendix 7. The expert systems are given in Electronic Appendices 8 and 9. A crosstab comparing our final classification with the 64 TWINSPAN clusters is given in Electronic Appendix 10.

Mean indicator values showed pronounced differences among the associations but also large overlaps (Electronic Appendix 11).

It should be noted that the area studied covered only a small part of the distribution of *Mesobromion*. Therefore, additional associations are expected outside the area studied. We defined the following associations within *Mesobromion* (letters are the same as in the ordination diagram; Fig. 3):

Association group M1: impoverished semi-dry grasslands in northwestern central Europe
(a) *Solidagini-Helictotrichetum* (only negatively differentiated by the absence of species that are at the limit of their northern distribution in central Europe; mainly found close to the Baltic sea, but similar stands also occur elsewhere; the soils are usually slightly acidic).

Association group M2: semi-dry grasslands in the lowlands in western central Europe
(b) *Gentiano-Koelerietum* (most widespread association of the alliance; traditionally used as sheep pastures).
(c) *Mesobrometum* (similar to the previous association, but dominated by *Bromopsis erecta*; usually mown).
(d) *Polygalo amarae-Seslerietum* (mesic *Sesleria caerulea* grasslands on steep slopes in low mountain ranges in Germany).

Association group M3: peri-Alpine semi-dry grasslands in western central Europe
(e) *Gentiano vernae-Brometum* (*Bromopsis erecta* meadows at high altitudes in the Jura Mountains and adjacent regions).
(f) *Carlino-Caricetum sempervirentis* (grasslands in the Bavarian Alps and their forelands).
(g) *Koelerio-Seslerietum* (mesic *Sesleria caerulea* grasslands in the Jura Mountains in SW Germany).

Within the alliance *Cirsio-Brachypodion* we defined the following associations (numbers are the same as in the ordination diagram; Fig. 3):

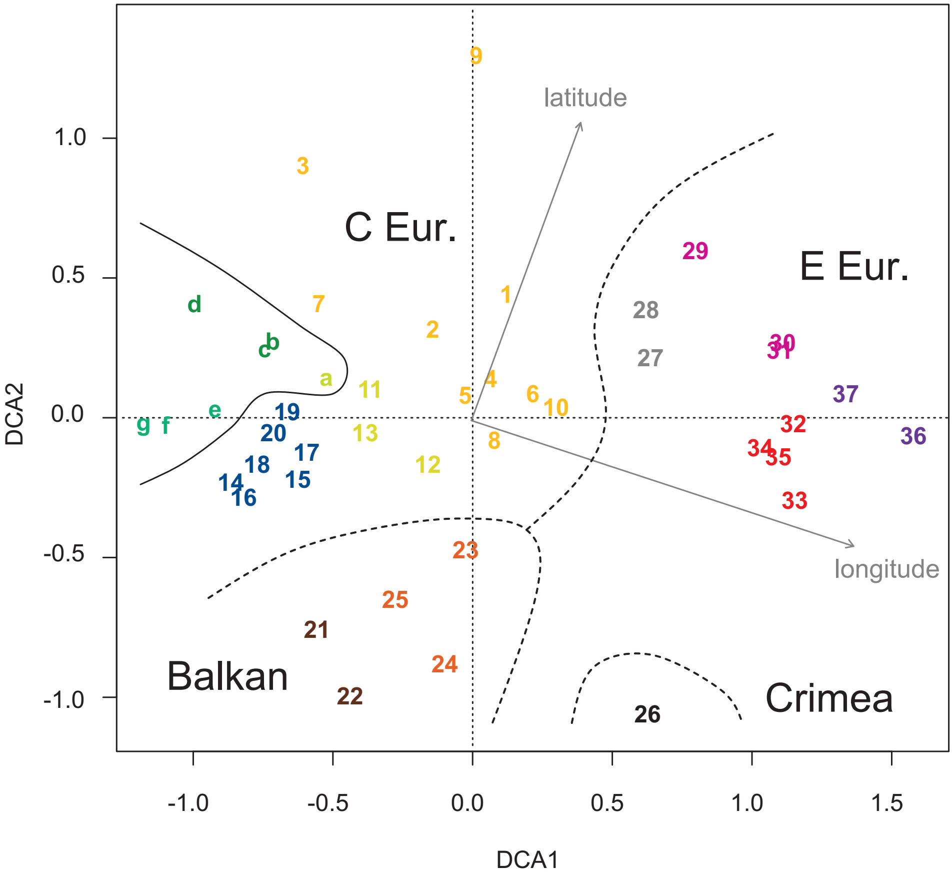

Fig. 3. – DCA ordination based on a constancy table of the associations. *Mesobromion*: a–g, *Cirsio-Brachypodion*: 1–37. Letters and numbers are the same as in the text and in the synoptic table (Electronic Appendix 6). Association groups are shown in different colours. The solid line represents the border between the two alliances. The dashed lines separate associations in central Europe (C Eur.), eastern Europe (E Eur.), the Balkans and Crimea. Mean longitude and mean latitude were passively projected onto the ordination diagram.

Association group C1: dry meadow steppes in central Europe

(1) *Adonido-Brachypodietum* (meadow steppes in NE central Europe; *Festuca stricta* subsp. *sulcata*, which is common in most associations of the alliance, is replaced by *Festuca stricta* subsp. *trachyphylla*).

(2) *Scabioso ochroleucae-Brachypodietum* (mainly distributed in Bohemia and central Germany; negatively differentiated by the absence of several Pannonian species).

(3) *Astragalo onobrychidis-Brometum* (meadow steppes in dry inner valleys in the Alps).

(4) *Inuletum ensifoliae* (meadow steppes in SE Poland).

(5) *Polygalo majoris-Brachypodietum* (meadow steppes in the Pannonian Basin and Transylvania, usually over calcareous bedrock).

(6) *Euphorbio pannonicae-Brachypodietum* (meadow steppes in the loess hills in the central Pannonian Basin; differentiated from the previous association by several loess specialists).
(7) *Cirsio pannonici-Seslerietum* (mesic *Sesleria caerulea* grasslands on steep slopes in Bohemia and central Germany).
(8) *Orchido militaris-Seslerietum heuflerianae* (mesic *Sesleria heuflerana* grasslands on steep, usually north-facing slopes in Transylvania, rarely also in E Slovakia and W Ukraine).
(9) *Genisto-Stipetum tirsae* (*Stipa tirsa* grasslands in W Germany; very few localities).
(10) *Stipetum tirsae* (all other *Stipa tirsa* grasslands in central Europe).

Association group C2: mesic meadow steppes in central Europe
(11) *Festuco rupicolae-Brometum* (usually dominated by *Bromopsis erecta*; otherwise only negatively differentiated from the following associations).
(12) *Brachypodio-Molinietum* (very species-rich grasslands in the Carpathian fringes on deep, loamy soils).
(13) *Colchico-Festucetum rupicolae* (slightly acidic grasslands dominated by *Festuca stricta* subsp. *sulcata*).

Association group C3: peri-Alpine semi-dry grasslands in eastern central Europe
(14) *Bromo-Plantaginetum* (species-rich calcareous grasslands in the NW Dinaric Mountains).
(15) *Euphorbio verrucosae-Caricetum montanae* (grasslands in the Eastern Alps on loamy soils).
(16) *Bromo-Danthonietum* (species rich grasslands in the NW Dinaric Mountains on slightly acid soils).
(17) “*Sesleria caerulea* community SK” (submontane mesic *Sesleria caerulea* grasslands in the Western Carpathians).
(18) “*Sesleria caerulea* community AT” (submontane mesic *Sesleria caerulea* grasslands in the Eastern Alps).
(19) *Carici albae-Brometum monocladi* (*Carex alba* grasslands in the Western Carpathians).
(20) “*Carex alba-Bromus erectus*-community” (*Carex alba* grasslands in the Eastern Alps).

Association group C4: meadow steppes in the western Balkans
(21) *Carici montanae-Brometum* (*Bromopsis erecta* grasslands in central and southern Serbia).
(22) “*Brometum erecti* SRB” (similar to the previous association, but at higher altitudes).

Association group C5: meadow steppes in the eastern Balkans
(23) *Hieracio pilosellae-Festucetum dalmaticae* (grasslands in W Bulgaria; *Festuca stricta* subsp. *sulcata* is replaced by *Festuca dalmatica*).
(24) *Galio lovcensis-Artemisietum chamaemelifoliae* (similar to the previous association, but on deeper soils).
(25) *Seslerietum latifoliae* (*Sesleria latifolia* grasslands in Bulgaria).

Association group C6: meadow steppes in Crimea
(26) *Adonido-Stipetum tirsae* (*Stipa tirsa* grasslands in E Crimea).

Association group C7: impoverished meadow steppes and steppe meadows
(27) *Salvio pratensis-Poetum angustifoliae* (meadow steppes in the forest-steppe zone in Ukraine, but probably also present elsewhere).
(28) *Artemisio campestris-Poetum angustifoliae* (steppe meadows in the forest zone in W Russia; only negatively differentiated).

Association group C8: calciphytic meadow steppes in eastern Europe
(29) *Asperulo cynanchicae-Onobrychidetum* (meadow steppes in W Russia on eroded slopes that are influenced by grazing).
(30) *Astero amelli-Potentilletum humifusae* (meadow steppes in W Russia on shallow soils mixed with gravel, usually mown).
(31) *Gentiano cruciatae-Stipetum* (meadow steppes in W Russia on eroded slopes with carbonate chernozem soils; only negatively differentiated from the previous two associations).

Association group C9: typical meadow steppes in eastern Europe
(32) *Veronico incanae-Inuletum ensifoliae* (meadow steppes in W Russia on southern slopes).
(33) *Vicio craccae-Centaureetum pseudophrygiae* (meadow steppes in W Russia on northern slopes).
(34) *Stipo tirsae-Bromopsietum ripariae* (meadow steppes in W Russia in flat upland positions).
(35) *Poo angustifoliae-Stipetum pennatae* (meadow steppes in the Southern Urals).

Association group C10: southern meadow steppes in eastern Europe
(36) *Serratulo radiatae-Stipetum pennatae* (meadow steppes at the southern margin of the forest-steppe zone in S Ukraine).
(37) *Trifolio alpestris-Stipetum tirsae* (meadow steppes at the southern margin of the forest-steppe zone in SW Russia).

Ordination

The DCA diagram mainly reflects the geographical locations of the associations (Fig. 3). The first axis corresponds to longitude and the second axis to latitude. The informal association groups are well separated in the diagram, with no overlaps between them. Interesting exceptions from the prevailing biogeographical pattern are the eccentric positions of *Astragalo onobrychidis-Brometum* and *Genisto-Stipetum tirsae* (both in the upper part of the diagram), which might at least partly be explained by the small number of relevés for both units, and the relatively central position of *Solidagini-Helictotrichetum* despite its marginal position in the area studied. The dry and mesic meadow steppes in the Pannonian region are separated from each other, with the second shifted to the left, which reflects its closer floristic relationship to *Mesobromion*. *Stipo tirsae-Bromopsietum ripariae* in the Kursk region and *Poo angustifoliae-Stipetum pennatae* in the Southern Urals are extremely close to each other, despite being separated by more than 1000 km.

Discussion

Alliance concepts

One of the most persistent problems in the syntaxonomy of European semi-dry grasslands is the delimitation between western *Mesobromion* and eastern *Cirsio-Brachypodion* (Illyés et al. 2007). Their diagnostic species groups overlap and several units have a transitional position between the two alliances, in particular the mesic meadow steppes in central Europe and peri-Alpine semi-dry grasslands in east-central Europe (association groups C2 and C3, Table 1), but also *Cirsio pannonici-Seslerietum*, which is the nomenclatural type of *Cirsio-Brachypodion* (Fig. 3). The best diagnostic taxa are *Festuca ovina* agg. (mostly *F. guestfalica*) for *Mesobromion* and *Festuca valesiaca* agg. (mostly *F. stricta* subsp. *sulcata*) for *Cirsio-Brachypodion*. Both *Festuca* taxa have a very high constancy and are almost completely mutually exclusive (Table 1). Therefore, the most natural and also the most practical delimitation between the two alliances is along the distribution border of these two grass taxa. A consequence of this alliance concept is that the number of positive diagnostic species that can be used in the formal definition of *Mesobromion* in that part of its range in the area studied is very small. Apart from *Festuca guestfalica*, it is mainly differentiated by the absence of diagnostic species of other alliances.

The delimitation of *Cirsio-Brachypodion* in the east is perhaps even more controversial than its delimitation in the west. So far, most authors have classified the meadow steppes in the eastern European forest-steppe zone in the alliance *Festucion valesiacae* (e.g. Poluyanov & Averinova 2012, Yamalov et al. 2012, Demina 2015). However, this classification cannot be maintained as the meadow steppes belong to the order *Brachypodietalia pinnati*, while *Festucion valesiacae* belongs to *Festucetalia valesiacae* (European grass steppes) (see also Willner et al. 2017b). Based on a type relevé from the Streletsky Steppe near Kursk, which belongs to *Stipo tirsae-Bromopsietum ripariae* in our classification, Royer (1991) described the alliance *Agrostio vinealis-Avenulion schellianae* for the eastern European meadow steppes. Independently, Korotchenko & Didukh (1997) described the alliance *Fragario viridis-Trifolion montani*, based on the *Salvio pratensis-Poetum angustifoliae*, the *locus classicus* of which is located in north-eastern Ukraine, less than 200 km from the Streletsky Steppe. Kuzemko et al. (2014) regard these two alliances as synonyms. Here, we follow the concept of Krausch (1961) who includes all eastern European meadow steppes in *Cirsio-Brachypodion*. The arguments in favour of this solution are as follows:

(i) The broadly defined *Cirsio-Brachypodion* has at least 14 character species (i.e. unique diagnostic species), of which 10 occur both in central and eastern Europe (Table 1), although most of them become more frequent towards the east. Only one of them (*Cirsium pannonicum*) is more frequent in central Europe. One character species (*Bromopsis riparia*) is common to eastern and south-eastern Europe, while two (*Dracocephalum ruyschiana*, *Pedicularis kaufmannii*) are restricted to eastern and one (*Polygala major*) to central Europe. If the alliance is split, *Cirsio-Brachypodion* sensu stricto would only have one or two character species and thus becomes a poorly characterized transition between continental meadow steppes and subatlantic *Mesobromion* grasslands.

(ii) The semi-dry grasslands in the forest zone in eastern Europe, also known as "steppe meadows", are described as a separate alliance *Scabioso ochroleucae-Poion angustifoliae* within the order *Galietalia veri*, class *Molinio-Arrhenatheretea* (Bulokhov

2001). However, our results clearly demonstrate that these grasslands belong to *Brachypodietalia pinnati*, as already proposed by Willner et al. (2017b). The content of this alliance corresponds to our association 28 (*Artemisio campestris-Poetum angustifoliae*), which, together with the type of *Fragario viridis-Trifolion montani* (association 27), forms the association group C7 (Table 1, Fig. 3). This group can hardly be assigned to either *Agrostio-Avenulion schellianae* or *Cirsio-Brachypodion* sensu stricto. It represents a central unit that is only defined by the absence of many diagnostic species. Thus, accepting the first two alliances would require the acceptance of *Fragario-Trifolion montani* (incl. *Scabioso-Poion*) as a third alliance. Moreover, for consistency, *Stipa tirsa* grasslands in Crimea (association group C6) would have to be accepted as the alliance *Adonido-Stipion tirsae*, and the grasslands in the Balkans (association groups C4 and C5) and perhaps also those in the Eastern Alps and NW Dinaric Mountains (association group C3) would also have to be raised to alliance level. This would lead to a large number of alliances with few or no character species.

A compromise between the varying alliance concepts could be to distinguish several suballiances within the broadly circumscribed *Cirsio-Brachypodion*. However, due to the still incomplete data coverage in eastern Europe, we regard a formal classification into suballiances as premature and prefer the informal association groups for describing the internal floristic structure of this alliance.

Another alliance that is separated from the *Cirsio-Brachypodion* by Royer (1991) is *Danthonio-Stipion stenophyllae*, described from Transylvania (Soó 1949). According to our formal definitions, the original content of this unit partly belongs to *Chrysopogono-Danthonion*, and partly to *Cirsio-Brachypodion*. With regard to the part assigned to *Cirsio-Brachypodion*, we could not even separate it at the level of associations from the communities in the western Pannonian region (i.e. *Stipetum tirsae* and *Brachypodio-Molinietum*). However, the type association of *Danthonio-Stipion*, *Agrostio-Danthonietum* (see Dengler et al. 2012), was assigned to *Chrysopogono-Danthonion*.

Scorzonerion villosae shares some diagnostic species with *Chrysopogono- Danthonion*, such as the grasses *Danthonia alpina* and *Chrysopogon gryllus*. On the other hand, it has several diagnostic species in common with *Mesobromion* and *Cirsio-Brachypodion*, like *Bromopsis erecta* and *Carex flacca*, and in particular with the peri-Alpine association groups within these two alliances (Table 1). *Hypochoeridenion maculatae*, which is described as a suballiance of *Scorzonerion villosae* (Terzi 2015), closely resembles our association group C3. As the location of the type of *Hypochoeridenion maculatae* is in north-eastern Italy, which is outside the area studied, we cannot provide a definite evaluation of this unit. However, it seems that the biogeographical pattern of the semi-dry grasslands in the Eastern Alps and Dinaric Mountains is similar to that of the Illyric beech forests (Willner et al. 2017a). The historical significance of this pattern should be further studied, e.g. by using phylogeographic methods.

Armerion elongatae represents semi-dry grasslands on sandy and siliceous soils, which are transitional between the classes *Festuco-Brometea* and *Koelerio-Corynephoretea*. It seems that the delimitation of these two classes is in need of revision and that the diagnostic species of these classes provided in Mucina et al. (2016), which were the basis for the selection of our data set, should also be revised. This alliance partly corresponds to *Koelerio-Phleion* (see e.g. Oberdorfer & Korneck 1978, Dúbravková et al. 2010).

Geographically vicariant associations and the limits of formal definitions

Species turn-over along geographical gradients, as found in our study, may be related to macroclimatic factors, but also, and in some cases even more so, to historical factors such as post-glacial migration and refugial history (Dullinger et al. 2012, Jiménez-Alfaro et al. 2018). Therefore, consistent differences in the species composition of communities in two regions, growing under otherwise similar habitat conditions, can be interpreted as a reflection of a different floristic history. Geographically vicariant associations are the syntaxonomic representation of such biogeographical hypotheses.

Our association group C1 (dry meadow steppes in central Europe) includes a typical example of geographically vicariant associations: *Adonido-Brachypodietum* (northeastern Germany, western and central Poland), *Scabioso ochroleucae-Brachypodietum* (central and southern Germany, Bohemia), *Inuletum ensifoliae* (southern Poland) and *Polygalo majoris-Brachypodietum* (Pannonian Basin, Transylvania). These units reflect the decline in steppe species from the Pannonian region towards the north and northwest. In addition to climatic differences, which undoubtedly exist between the regions, historical processes might be responsible for the observed floristic gradients, such as (i) delayed immigration of thermophilous species from glacial refugia in south-eastern Europe (Magyari et al. 2010), or (ii) regional extinction of steppe species during the "mid-Holocene bottleneck" due to the spread of deciduous forests in some parts of central Europe, but survival of steppe in other parts (Pokorný et al. 2015). Which of these factors plays the main role is not clear, but recent studies on the phylogeography of steppe species indicate that the second process is probably more important than previously thought (Kajtoch et al. 2016, Plenk et al. 2017).

To a large extent we were able to reproduce the traditional delimitation of the aforementioned associations using our expert system (Fig. 4). Nevertheless, a considerable number of plots were assigned to a "wrong" association in terms of geographical location. For instance, there are relevés within the distribution range of *Polygalo majoris-Brachypodietum* that lack the diagnostic species of this association and were therefore assigned to *Inuletum ensifoliae* or *Scabioso ochroleucae-Brachypodietum*. However, we suspect that in many cases the "missing" diagnostic species will be present somewhere near the sample plots, perhaps even within the same patch of grassland. Another possibility is that, in addition to biogeographical history, other local gradients in site conditions or landscape history may result in the occurrence of dry meadow steppes resembling *Scabioso ochroleucae-Brachypodietum* outside its main distribution range. In Hungary, two such units are reported by Lengyel et al. (2016): *Sanguisorbo minoris-Brometum* and "*Linum tenuifolium-Brachypodium pinnatum*-type". While we were not able to reproduce them as separate associations, most of their content was assigned to *Scabioso ochroleucae-Brachypodietum* by our expert system. Further studies might be necessary to clarify the syntaxonomic affiliation of dry meadow steppes in the Pannonian Basin that lack the characteristic species of *Polygalo majoris-Brachypodietum*.

Regardless of such "hidden" differences in external factors, a certain amount of misclassified relevés is probably unavoidable unless geographically vicariant associations are merged into rather broad and heterogeneous units with very large distribution ranges. In addition, the definition of ecologically vicariant units could hardly be sharper – the mismatch between species composition and external factors is just more obvious

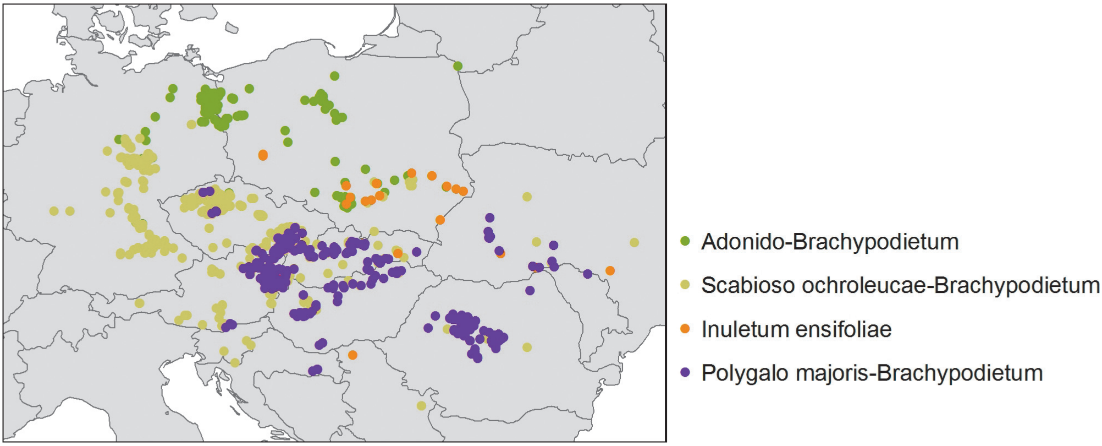

Fig. 4. – Examples of four geographically vicariant associations. Note that the dots partly overlap. Individual maps for all associations are given in Electronic Appendix 7.

along geographical gradients. Willner (2006) regards 10% misclassified plots as acceptable, and our classification scheme seems to be within this limit. However, under the premise that sympatric associations should be clearly different in terms of habitat conditions, formalistic assignment of plots using supra-regional expert systems is unlikely to ever give fully satisfying results.

An additional problem in defining geographical units (both associations and higher syntaxa) is that species of a particular fidelity are not automatically suitable as diagnostic species. Different proportions of ecological subunits in two regions may bias the constancy of species. For example, several species indicating acidic soils of high fidelity for *Chrysopogono-Danthonion* are widely distributed all over central Europe (e.g. *Hypochaeris radicata*, *Trifolium ochroleucon*, *Viola tricolor*). Using these species in the formal definition of the alliances resulted in plots from Germany being assigned to the Balkan alliance, which obviously is not appropriate if the classification is supposed to reflect a biogeographical gradient. Problems also occur if ecologically defined units have different abundances in different regions, leading to biased constancy values of species with geographically restricted ranges. These effects can be mitigated by careful stratification of the dataset (Lengyel et al. 2011), but probably not completely avoided. Therefore, an additional criterion for diagnostic species might be necessary: A species should only be considered as diagnostic for a vegetation unit if it is indicative of the external (ecological or biogeographical) factors that are to be reflected in the classification. A simple test for the suitability of a diagnostic species to discriminate two vegetation units is to compare the environmental amplitude or the geographical range of the species with the amplitude or range of the vegetation units. If a unit is restricted to south-eastern Europe, but the species has a much larger range, then the latter is unsuitable as differential species for this vegetation unit.

Similarity of semi-dry grasslands in central and eastern Europe

One of the important results of our study is that it reveals that semi-dry grasslands in central Europe are quite similar to meadow steppes in eastern Europe. This finding is interesting both from biogeographical and methodological points of view. We believe that for the understanding of the distribution and reconstruction of the history of the European semi-dry grasslands, it is highly relevant that the species pool of these grasslands is largely shared across vast territories in Eurasia, in a broad belt along the 50th parallel. For example, 29 of the 30 species with the highest frequency in the association *Poo angustifoliae-Stipetum pennatae* in the Southern Urals region (i.e. on the eastern margin of the area studied) are very common in central European semi-dry grasslands (e.g. *Fragaria viridis*, *Plantago media*, *Galium verum*, *Filipendula vulgaris*, *Trifolium montanum, Galium boreale*) (see Electronic Appendix 6, association C35), while one species (*Phlomis tuberosa*) is present but rare in central Europe. Many of these species also occur in forest fringes (*Trifolio-Geranietea sanguinei*) and in open-canopy forests (*Quercetea pubescentis*, *Brachypodio pinnati-Betuletea pendulae*) in both regions and may be considered a part of an ancient species pool of hemiboreal and forest-steppe communities. As hypothesized earlier (e.g. Nimis et al. 1994, Chytrý et al. 2010, Korotchenko & Kagalo 2012, Roleček et al. 2014), this large species pool may be inherited from the light-demanding and semi-shade communities of the late Pleistocene and early Holocene, when they were widespread across Eurasia. We assume that their survival was possible particularly in the lowland regions where open or semi-open habitats were available throughout the Holocene, despite the expansion of closed canopy forests. According to recent views, central Europe, with its diverse topography, regional climates and variable histories of human settlement, provided such refuges (Magyari et al. 2010, Hájková et al. 2011, Pokorný et al. 2015, Feurdean et al. 2018). Apart from colder winters, the forest-steppe zone in eastern Europe has a climate essentially similar to the drier regions in central Europe (Feddema 2005). Thus, the broad distribution of *Cirsio- Brachypodion* grasslands may be interpreted as a result of the former broad distribution of ancestral forest-steppe communities and relict survival of their characteristic species in a number of places between central Europe and the Southern Urals.

Methodological considerations

In numerical vegetation classification a frequent experience is that extending the geographical coverage of a study results in similarity-based multivariate methods giving less satisfactory results at low hierarchical levels. Among association-level analyses the geographical range of our study is extremely broad. However, the large sample size seriously constrained our choice of statistical methods. We have opted for an expert- based classification, which was elaborated by informally confronting several numerical classifications performed on the total study area and its subregions (usually countries), as well as with literature data. For all numerical classifications we used the TWINSPAN method using the WinTWINS 2.3 programme, which can handle such a large data table and usually provides robust and well-interpretable clusters at the higher hierarchical levels, which correspond to one or a few main gradients of compositional variation. With the cross-checks of classifications based on different data subsets, we also aimed at reducing the well-known drawbacks of TWINSPAN, that is, the rigidly dichotomous topology of the dendrogram (Roleček et al. 2009), and the low performance of classifications with a high number of clusters (Lötter et al. 2013). Moreover, the association concept applied in the present paper is based on the idea that vegetation units should reflect a correlation between species composition and external factors (Willner 2006). Thus, our main aim was the identification of units that presumably differ in site conditions and/or geographical distribution, and of establishing unambiguous floristic definitions for them, while the choice of the multivariate classification method was less important.

See www.preslia.cz for Electronic Appendices 1–11

Conclusions

We present the first large-scale revision of European semi-dry grasslands of the order *Brachypodietalia pinnati* using formal definitions of vegetation units. All the described grassland types are of great conservation value, and a consistent and harmonised classification based on unambiguously defined units will help develop inventories and maps for their effective protection at the European scale. Formal definitions of vegetation units are also essential if we want to use the phytosociological system to formulate ecological and biogeographical hypotheses. In this way, syntaxonomy is helping to enhance our understanding of European grassland vegetation.

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Souhrn

Širokolisté suché trávníky Eurasie patří k druhově nejbohatším a ochranářsky nejhodnotnějším biotopům severní polokoule. Předkládaná syntaxonomická syntéza je založena na 34 173 fytocenologických snímcích klasifikovaných do třídy *Festuco-Brometea* pomocí diagnostických druhů uvedených v evropském přehledu vyšších vegetačních jednotek (EuroVegChecklist; Mucina et al. 2016). Pro nalezení diagnostických druhů řádů této třídy jsme použili datový soubor klasifikovaný pomocí algoritmu TWINSPAN. 15 449 snímků bylo zařazeno do řádu *Brachypodietalia pinnati*, který odpovídá širokolistým suchým trávníkům. Tento podsoubor byl dále klasifikován stejnou metodou. Vytvořili jsme formální definice pro následující svazy: *Mesobromion erecti*, *Cirsio-Brachypodion pinnati* (zahrnuje *Fragario-Trifolion montani*, *Agrostio-Avenulion schellianae*, *Scabioso ochroleucae-Poion angustifoliae* a *Adonido vernalis-Stipion tirsae*), *Scorzonerion villosae* a *Chrysopogono-Danthonion*. Svaz *Armerion elongatae* považujeme za přechodný k třídě *Koelerio-Corynephoretea* a jeho postavení vyžaduje další studium. Vytvořili jsme též formální definice pro všechny asociace svazů *Mesobromion* a *Cirsio-Brachypodion* vyskytující se v zájmové oblasti. Asociace byly identifikovány s využitím (i) klasifikace celého řádu algoritmem TWINSPAN, (ii) klasifikace regionálně vymezených podsouborů (obvykle obsahujících všechny snímky řádu *Brachypodietalia* pocházející z dané země) stejnou metodou a (iii)

stávajících národních vegetačních přehledů. Pro všechny formální definice byl použit formát expertního systému v programu JUICE. Vztahy mezi rozlišenými asociacemi a hlavní gradienty v jejich druhovém složení byly zobrazeny pomocí detrendované korespondenční analýzy. Naše výsledky ukazují, že luční stepi lesostepní zóny východní Evropy jsou velmi podobné širokolistým suchým trávníkům východní části střední Evropy, což zřejmě odráží jejich společný původ v glaciálních a staroholocenních lesostepních společenstvech.

References

Aćić S., Petrović M., Dajić Stevanović Z. & Šilc U. (2012) Vegetation database Grassland vegetation in Serbia. – Biodiversity & Ecology 4: 418.

Borhidi A. (1995) Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. – Acta Botanica Hungarica 39: 97–181.

Braun-Blanquet J. (1936) Über die Trockenrasengesellschaften des *Festucion vallesiacae* in den Ostalpen. – Berichte der Schweizerischen Botanischen Gesellschaf 46: 169–189.

Braun-Blanquet J. & Tüxen R. (1943) Übersicht der höheren Vegetationseinheiten Mitteleuropas (unter Ausschluss der Hochgebirge). – Communication la Station Internationale de Géobotanique Méditerraneénne et Alpine de Montpellier 84: 1–11.

Bulokhov A. D. (2001) Travyanaya rastitel'nost' Yugo-Zapadnogo Nechernozemia Rossii [Herbaceous vegetation of the South-West Non-chernozem Region of Russia]. – Bryanskii gosudarstvennyi universitet, Bryansk.

Chytrý M., Danihelka J., Horsák M., Kočí M., Kubešová S., Lososová Z., Otýpková Z., Tichý L., Martynenko V. B. & Baisheva E. Z. (2010) Modern analogues from the Southern Urals provide insights into biodiversity change in the early Holocene forests of Central Europe. – Journal of Biogeography 37: 767–780.

Chytrý M., Dražil T., Hájek M., Kalníková V., Preislerová Z., Šibík J., Ujházy K., Axmanová I., Bernátová D., Blanár D., Dančák M., Dřevojan P., Fajmon K., Galvánek D., Hájková P., Herben T., Hrivnák R., Janeček Š., Janišová M., Jiráská Š., Kliment J., Kochjarová J., Lepš J., Leskovjanská A., Merunková K., Mládek J., Slezák M., Šeffer J., Šefferová V., Škodová I., Uhlířová J., Ujházyová M. & Vymazalová M. (2015) The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). – Preslia 87: 217–278.

Chytrý M., Hennekens S. M., Jiménez-Alfaro B., Knollová I., Dengler J., Jansen F., Landucci F., Schaminée J. H. J., Aćić S., Agrillo E., Ambarlı D., Angelini P., Apostolova I., Attorre F., Berg C., Bergmeier E., Biurrun I., Botta-Dukát Z., Brisse H., Campos J. A., Carlón L., Čarni A., Casella L., Csiky J., Ćušterevska R., Stevanoviă Z. D., Danihelka J., De Bie E., de Ruffray P., De Sanctis M., Dickoré W. B., Dimopoulos P., Dubyna D., Dziuba T., Ejrnæs R., Ermakov N., Ewald J., Fanelli G., Fernández-González F., FitzPatrick Ú., Font X., García-Mijangos I., Gavilán R. G., Golub V., Guarino R., Haveman R., Indreica A., Işık Gürsoy D., Jandt U., Janssen J. A. M., Jiroušek M., Kącki Z., Kavgacý A., Kleikamp M., Kolomiychuk V., Krstivojević-Ćuk M., Krstonošić D., Kuzemko A., Lenoir J., Lysenko T., Marcenò C., Martynenko V., Michalcová D., Moeslund J. E., Onyshchenko V., Pedashenko H., Pérez-Haase A., Peterka T., Prokhorov V., Rašomavičius V., Rodríguez-Rojo M. P., Rodwell J. S., Rogova T., Ruprecht E., Rūsiņa S., Seidler G., Šibík J., Šilc U., Škvorc Ž., Sopotlieva D., Stančić Z., Svenning J. C., Swacha G., Tsiripidis I., Turtureanu P. D., Uğurlu E., Uogintas D., Valachovič M., Vashenyak Y., Vassilev K., Venanzoni R., Virtanen R., Weekes L., Willner W., Wohlgemuth T. & Yamalov S. (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. – Applied Vegetation Science 19: 173–180.

Chytrý M. & Rafajová M. (2003) Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. – Preslia 75: 1–15.

Chytrý M., Tichý L., Holt J. & Botta-Dukát J. (2002) Determination of diagnostic species with statistical fidelity measures. – Journal of Vegetation Science 13: 79–90.

Demina O. (2015) Klassifikatsiya rastiteľnosti stepei basseina Dona [Classification of the steppe vegetation of the Don basin]. – Izdateľstvo Yuzhnogo federaľnogo universiteta, Rostov-na-Donu.

Dengler J. (2003) Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation. – Martina Galunder-Verlag, Nümbrecht.

Dengler J., Becker T., Ruprecht E., Szabó A., Becker U., Beldean M., Bita-Nicolae C., Dolnik C., Goia I., Peyrat J., Sutcliffe L. M. E., Turtureanu P. D. & Uğurlu E. (2012) *Festuco-Brometea* communities of the Transylvanian Plateau (Romania): a preliminary overview on syntaxonomy, ecology, and biodiversity. – Tuexenia 32: 319–359.

Dengler J., Berg C., Eisenberg M., Isermann M., Jansen F., Koska I., Löbel S., Manthey M., Päzolt J., Spangenberg A., Timmermann T. & Wollert H. (2003) New descriptions and typifications of syntaxa within the project Plant communities of Mecklenburg-Vorpommern and their vulnerability Part I. – Feddes Repertorium 114: 587–631.

Dengler J. & Rūsiņa S. (2012) Database Dry Grasslands in the Nordic and Baltic Region. – Biodiversity & Ecology 4: 319–320.

Dierschke H. (1997) Pflanzensoziologisch-synchorologische Stellung des Xerothermgraslandes (*Festuco-Brometea*) in Mitteleuropa. – Phytocoenologia 27: 127–140.

Dúbravková D., Chytrý M., Willner W., Illyés E., Janišová M. & Kállayné Szerényi J. (2010) Dry grasslands in the Western Carpathians and the northern Pannonian Basin a numerical classification. – Preslia 82: 165–221.

Dullinger S., Willner W., Plutzar C., Englisch T., Schratt-Ehrendorfer L., Moser D., Ertl S., Essl F. & Niklfeld H. (2012) Post-glacial migration lag restricts range filling of plants in the European Alps. – Global Ecology and Biogeography 21: 829–840.

Feddema J. J. (2005) A revised Thornthwaite-type global climate classification. – Physical Geography 26: 442–466.

Feurdean A., Ruprecht E., Molnár Z., Hutchinson S. M. & Hickler T. (2018) Biodiversity-rich European grasslands: ancient, forgotten ecosystems. – Biological Conservation 228: 224–232.

Filatova T. D., Zolotukhin N. I. & Poluyanov A. V. (2014) Steppe and meadow vegetation. – In: Vlasov A. A., Vlasova O. P., Zolotukhin N. I., Ryzhkov O. V., Soshnina V. P. & Filatova T. D. (eds), The Streletsky site of the Central Chernozem Reserve: a field guide, p. 41–57, The Central Chernozem State Biosphere Nature Reserve named after Professor V. V. Alyokhin, Kursk.

Fischer H. S. (2015) On the combination of species cover values from different vegetation layers. – Applied Vegetation Science 18: 169–170.

Hájková P., Roleček J., Hájek M., Horsák M., Fajmon K., Polák M. & Jamrichová E. (2011) Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts (Czech Republic and Slovakia). – Preslia 83: 185–204.

Hill M. O. & Šmilauer P. (2005) TWINSPAN for Windows version 2.3. – Centre for Ecology & Hydrology, Huntingdon, and University of South Bohemia, České Budějovice.

Horvat I., Glavač V. & Ellenberg H. (1974) Vegetation Südosteuropas. – Gustav Fischer Verlag, Stuttgart.

Hülber K., Moser D., Sauberer N., Maas B., Staudinger M., Grass V., Wrbka T. & Willner W. (2017) Plant species richness decreased in semi-natural grasslands in the Biosphere Reserve Wienerwald, Austria, over the past two decades, despite agri-environmental measures. – Agriculture, Ecosystems and Environment 243: 10–18.

Illyés E., Chytrý M., Botta-Dukát Z., Jandt U., Škodová I., Janišová M.,Willner W. & Hájek O. (2007) Semi-dry grasslands along a climatic gradient across Central Europe: vegetation classification with validation. – Journal of Vegetation Science 18: 835–846.

Jandt U. & Bruelheide H. (2012) German Vegetation Reference Database (GVRD). – Biodiversity & Ecology 4: 355.

Jansen F., Dengler J. & Berg C. (2012) VegMV – the vegetation database of Mecklenburg-Vorpommern. – Biodiversity & Ecology 4: 149–160.

Janssen J. A. M., Rodwell J. S., García Criado M., Gubbay S., Haynes T., Nieto A., Sanders N., Landucci F., Loidi J., Ssymank A., Tahvanainen T., Valderrabano M., Acosta A., Aronsson M., Arts G., Attorre F., Bergmeier E., Bijlsma R.-J., Bioret F., Biţă-Nicolae C., Biurrun I., Calix M., Capelo J., Čarni A., Chytrý M., Dengler J., Dimopoulos P., Essl F., Gardfjell H., Gigante D., Giusso del Galdo G., Hájek M., Jansen F., Jansen J., Kapfer J., Mickolajczak A., Molina J. A., Molnár Z., Paternoster D., Piernik A., Poulin B., Renaux B., Schaminée J. H. J., Šumberová K., Toivonen H., Tonteri T., Tsiripidis I., Tzonev R. & Valachovič M. (2016) European Red List of Habitats. Part 2. Terrestrial and freshwater habitats. – Publications Office of the European Union, Luxembourg.

Jiménez-Alfaro B., Girardello M., Chytrý M., Svenning J.-C., Willner W., Gégout J.-C., Agrillo E., Campos J. A., Jandt U., Kącki Z., Šilc U., Slezák M., Tichý L., Tsiripidis I., Turtureanu P. D., Ujházyová M. & Wohlgemuth T. (2018) History and environment shape species pools and community diversity in European beech forests. – Nature Ecology & Evolution 2: 483–490.

Kajtoch Ł., Cieślak E., Varga Z., Paul W., Mazur M. A., Sramkó G. & Kubisz D. (2016) Phylogeographic patterns of steppe species in Eastern Central Europe: a review and the implications for conservation. – Biodiversity & Conservation 25: 1–31.

Klika J. (1939) Die Gesellschaften des *Festucion vallesiacae*-Verbandes in Mitteleuropa. – Studia Botanica Čechica 2/3: 117–157.

Klika J. & Hadač E. (1944) Rostlinná společenstva Střední Evropy [Plant communities of Central Europe]. – Příroda 36/8–9: 1–26.

Korneck D. (1974) Xerothermvegetation von Rheinland-Pfalz und Nachbargebieten. – Schriftenreihe für Vegetationskunde 7: 5–196.

Korotchenko I. A. & Didukh Y. P. (1997) Stepova roslynnłsť pivdennoyi chastyny Livoberezhnogo Lisostepu Ukrayiny. II. Klas *Festuco-Brometea* [The steppe vegetation of the southern part of the Left-Bank Forest-Steppe of Ukraine. II. Class *Festuco-Brometea*]. – Ukrayinskyi fłtocenologichnyi zbirnik, Ser. A, 1: 20–39.

Korotchenko I. A. & Kagalo À. À. (2012) Ekologicheskie osobennosti stepnoy rastitelnosti Zapadnogo Podolya (Ukraina) [Ecological peculiarities of steppe vegetation of Western Podolia (Ukraine)]. – Izvestiya Samarskogo nauchnogo tsentra Rossiyskoy akademii nauk 14: 1477–1480.

Krausch H.-D. (1961) Die kontinentalen Steppenrasen (*Festucetalia vallesiacae*) in Brandenburg. – Feddes Repertorium Beihefte 139: 167–227.

Kuneš P., Svobodová-Svitavská H., Kolář J., Hajnalová M., Abraham V., Macek M., Tkáč P. & Szabó P. (2015) The origin of grasslands in the temperate forest zone of east-central Europe: long-term legacy of climate and human impact. – Quaternary Science Reviews 116: 15–27.

Kuzemko A. (2012) Ukrainian Grasslands Database. – Biodiversity & Ecology 4: 430.

Kuzemko A., Becker T., Didukh Y. P., Ardelean I. V., Becker U., Beldean M., Dolnik C., Jeschke M., Naqinezhad A., Uğurlu E., Ünal A., Vassilev K., Vorona E. I., Yavorska O. H. & Dengler J. (2014) Dry grassland vegetation of Central Podolia (Ukraine): a preliminary overview of its syntaxonomy, ecology and biodiversity. – Tuexenia 34: 391–430.

Landucci F., Tichý L., Šumberová K. & Chytrý M. (2015) Formalized classification of species-poor vegetation: a proposal of a consistent protocol for aquatic vegetation. – Journal of Vegetation Science 26: 791–803.

Lengyel A., Chytrý M. & Tichý L. (2011) Heterogeneity-constrained random resampling of phytosociological databases. – Journal of Vegetation Science 22: 175–183.

Lengyel A., Illyés E., Bauer N., Csiky J., Király G., Purger D. & Botta-Dukát Z. (2016) Classification and syntaxonomical revision of mesic and semi-dry grasslands in Hungary. – Preslia 88: 201–228.

Lötter M. C., Mucina L. & Witkowski E. T. F. (2013) The classification conundrum: species fidelity as leading criterion in search of a rigorous method to classify a complex forest data set. – Community Ecology 14: 121–132.

Magyari E. K., Chapman J. C., Passmore D. G., Allen J. R. M., Huntley J. P. & Huntley B. (2010) Holocene persistence of wooded steppe in the Great Hungarian Plane. – Journal of Biogeography 37: 915–935.

Mucina L., Bültmann H., Dierßen K., Theurillat J.-P., Raus T., Čarni A., Šumberová K., Willner W., Dengler J., Gavilán R., Chytrý M., Hájek M., Di Pietro R., Pallas J., Daniëls F., Bergmeier E., Guerra A., Ermakov N., Valachovič M., Schaminée J., Lysenko T., Didukh Y., Pignatti S., Rodwell J., Capelo J., Weber H., Dimopoulos P., Aguiar C., Hennekens S. & Tichý L. (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. – Applied Vegetation Science 19 (Suppl. 1): 3–264.

Nimis P. L., Malyshev L. I. & Bolognini G. (1994) A phytogeographic analysis of birch woodlands in the southern part of West Siberia. – Vegetatio 113: 25–39.

Oberdorfer E. & Korneck D. (1978) Klasse *Festuco-Brometea* Br.-Bl. et Tx. 43. – In: Oberdorfer E. (ed.), Süddeutsche Pflanzengesellschaften, 2. Aufl., Teil II. Gustav Fischer Verlag, Stuttgart.

Plenk K., Bardy K., Höhn M., Thiv M. & Kropf M. (2017) No obvious genetic erosion, but evident relict status at the westernmost range edge of the Pontic-Pannonian steppe plant *Linum flavum* L. (*Linaceae*) in Central Europe. – Ecology & Evolution 7: 6527–6539.

Pokorný P., Chytrý M., Juřičková L., Sádlo J., Novák J. & Ložek V. (2015) Mid-Holocene bottleneck for central European dry grasslands: did steppe survive the forest optimum in northern Bohemia, Czech Republic? – The Holocene 25: 716–726.

Poluyanov A. V. & Averinova E. A. (2012) Travyanaya rastiteľnosť Kurskoi oblasti: sintaksonomiya i voprosy okhrany [Grassland vegetation of the Kursk region: syntaxonomy and conservation issues]. – Kurskii Gosudarstvennyi Universitet, Kursk.

Poschlod P. & WallisDeVries M. F. (2002) The historical and socioeconomic perspective of calcareous grasslands – lessons from the distant and recent past. – Biological Conservation 104: 361–376.

Roleček J., Čornej I. I. & Tokarjuk A. I. (2014) Understanding the extreme species richness of semi-dry grasslands in east-central Europe: a comparative approach. – Preslia 86: 13–34.

Roleček J., Tichý L., Zelený D. & Chytrý M. (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. – Journal of Vegetation Science 20: 596–602.

Royer J. M. (1991) Synthèse eurosibérienne, phytosociologique et phytogéographique de la classe des *Festuco-Brometea*. – Dissertationes Botanicae 178: 1–296.

Soó R. (1949) Les associations végétales de la Moyenne-Transylvanie. II. Les associations des marais, des prairies et des steppes. – Acta Geobotanica Hungarica 6/2: 1–107.

Terzi M. (2015) Numerical analysis of the order *Scorzoneretalia villosae*. – Phytocoenologia 45: 11–32.

Theurillat J.-P., Terzi M. & Di Pietro R. (2017) Proposal (22): to conserve the name *Mesobromion erecti* (Br.-Bl. et Moor 1938) Oberd. 1957 against the name *Bromion erecti* W. Koch 1926. – Phytocoenologia 47: 385–387.

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

Vassilev K., Ruprecht E., Alexiu V., Becker T., Beldean M., Biţă-Nicolae C., Csergő A. M., Dzhovanova I., Filipova E., Frink J. P., Gafta D., Georgieva M., Germany M. S., Goia I., Gumus M., Hennekens S. M., Janišová M., Knollová I., Koleva V., Kostadinova S., Kuzmanović N., Loos J., Mardari C., Michl T., Neblea M. A., Nicoară R. I., Novák P., Öllerer K., Onete M., Palpurina S., Paulini I., Pedashenko H., Puşcaş M., Roman A., Šibík J., Sîrbu C., Stancu D. I., Sutcliffe L., Szabó A., Tomescu C.-V., Totev E., Tsvetanov B., Turtureanu P. D., Vassileva P., Velev N. & Dengler J. (2018) The Romanian Grassland Database (RGD): historical background, current status and future perspectives. – Phytocoenologia 48: 91–100.

Veen P., Jefferson R., de Smidt J. & van der Straaten J. (eds) (2009) Grasslands in Europe of high nature value. – KNNV Publishing, Zeist, Netherlands.

Walter H. (1974) Die Vegetation Osteuropas, Nord- und Zentralasiens. – Gustav Fischer Verlag, Stuttgart.

Weber H. E., Moravec J. & Theurillat J.-P. (2000) International code of phytosociological nomenclature. 3rd edition. – Journal of Vegetation Science 11: 739–768.

Willner W. (2006) The association concept revisited. – Phytocoenologia 36: 67–76.

Willner W., Jiménez-Alfaro B., Agrillo E., Biurrun I., Campos J. A., Čarni A., Casella L., Csiky J., Ćušterevska R., Didukh Ya. P., Ewald J., Jandt U., Jansen F., Kącki Z., Kavgacý A., Lenoir J., Marinšek A., Onyshchenko V., Rodwell J. S., Schaminée J. H. J., Šibík J., Škvorc Ž., Svenning J.-C., Tsiripidis I., Turtureanu P. D., Tzonev R., Vassilev K., Venanzoni R., Wohlgemuth T. & Chytrý M. (2017a) Classification of European beech forests: a Gordian Knot? – Applied Vegetation Science 20: 494–512.

Willner W., Kuzemko A., Dengler J., Chytrý M., Bauer N., Becker T., Biţă-Nicolae C., Botta-Dukát Z., Čarni A., Csiky J., Igić R., Kącki Z., Korotchenko I., Kropf M., Krstivojević-Ćuk M., Krstonošić D., Rédei T., Ruprecht E., Schratt-Ehrendorfer L., Semenishchenkov Y., Stančić Z., Vashenyak Y., Vynokurov D. & Janišová M. (2017b) A higher-level classification of the Pannonian and western Pontic steppe grasslands (Central and Eastern Europe). – Applied Vegetation Science 20: 143–158.

Willner W., Tichý L. & Chytrý M. (2009) Effects of different fidelity measures and contexts on the determination of diagnostic species. – Journal of Vegetation Science 20: 130–137.

Wilson J. B., Peet R. K., Dengler J. & Pärtel M. (2012) Plant species richness: the world records. – Journal of Vegetation Science 23: 796–802.

Yamalov S. M., Martynenko V. B., Abramova L. M., Golub V. B., Baisheva E. Z. & Bayanov A. V. (2012) Prodromus rastitel'nykh soobshchestv Respubliki Bashkortostan [Prodromus of the Plant Communities of Bashkortostan Republic]. – Gilem, Ufa.

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