



Tall herb-rich steppe in the peri-Carpathian region of Ukraine and Romania

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Abstract

Aim: Forest-steppe complexes in the peri-Carpathian region harbour specific vegetation dominated by tall herbs. Our aim was to provide new phytosociological data on this vegetation type from the Ukraine and adjacent parts of Romania, compare it with previously published data, discuss its position in broad ecological and biogeographical context and suggest its syntaxonomic treatment respecting both its physiognomy and species composition. **Study area:** Western Ukraine and Romania. **Methods:** We assembled a dataset of 711 relevés of thermophilous herb-rich vegetation (*Trifolio-Geranietea*) from the study area and adjacent regions of Eastern Poland and Slovakia using own field research, literature survey and large databases. Using intersection of three different classification algorithms (beta-flexible, modified TWINSPAN and K-means clustering) we identified a consensus delimitation of the vegetation type. NMDS ordination, analysis of diagnostic, constant and dominant species, and Didukh indicator values were used to characterize its species composition and habitat conditions. **Results:** Altogether 58 relevés from Western Ukraine and Romania were classified to a tall herb-dominated vegetation type that we identified with the association *Trollio-Clematidetum recti* Täuber et Weber 1976 described from Romania. We assigned it to the alliance *Geranion sanguinei*. It differs from other communities of this alliance in its preference for shady slopes, greater stand height and considerable representation of mesophilous and montane species. It is confined to calcareous bedrock with high soil pH and high mineral richness. **Conclusions:** We suggest that the studied tall herb-dominated vegetation is a specific steppe type, confined to relatively moist and nutrient rich sites in the peri-Carpathian area. Analogous vegetation occurs in the Alps, Balkans, hemiboreal Europe, South Urals and Western Siberia. Its species composition and biogeographical relationships provide further support for the hypothesis that steppe meadows of Central Europe, including tall herb-dominated stands, are linked to the Pleistocene and early-Holocene forest-steppe of temperate Eurasia.

Keywords: fringe vegetation; peri-Carpathian; relict; steppe meadows; syntaxonomy; tall forbs; tall herbs; *Trifolio-Geranietea*; vegetation diversity

Taxonomic reference: Euro+Med (2021) [last accessed 3 March 2021] for vascular plants

Syntaxonomic reference: Mucina et al. (2016) for higher syntaxa

Abbreviations: NMDS = Non-Metric Multidimensional Scaling

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Introduction

In the regions where climate, habitat heterogeneity or disturbance regimes facilitate co-existence of forests and steppe grasslands, diverse vegetation complexes may develop. These complexes may include plant assemblages composed of forest species, dry grassland species, and also species of transitional habitats, i.e. heliophilous and semi-shade species which are not adapted to very dry

soils. The latter group may occur in open-canopy forests (most often dominated by oaks and pines), scrub or semi-dry grasslands. Under favourable conditions herb-dominated communities may also develop. These are often called “fringe vegetation” (referring to forest fringes where they frequently occur) and classified to a phytosociological class *Trifolio-Geranietea sanguinei*.

Vegetation complexes including the mentioned vegetation types were famously described as “Steppenheide” by

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Gradmann (1898) from the Swabian Alb in south-western Germany. Müller (1962) pointed out that the most characteristic component of Steppenheide is fringe vegetation, for which he proposed a robust syntaxonomic scheme. Authors of the studies reviewed by Müller (1962) agreed that fringe communities should be best developed in Eastern Europe, as they occur in forest-steppe complexes which are typical for the regions with more continental climate. Since that time, extensive evidence has been accumulated about the diversity of fringe vegetation across Europe (Mucina et al. 2016), including the forest-steppe regions of Eastern Europe (e.g. Bulokhov & Kharin 2008, Yamalov & Kucherova 2009, Averinova & Poluyanov 2011).

Nevertheless, we still can see inconsistencies in the understanding of fringe vegetation. For example, while most national vegetation surveys in Central and Eastern Europe accept Müller's class *Trifolio-Geranietea* (e.g. Mucina et al. 1993, Matuskiewicz 2007, Coldea 2012, Hegedűsová Vantarová & Škodová 2014, Dubyna & Dzyuba 2019), some authors (e.g. Chytrý et al. 2007, Borhidi et al. 2012) classify fringe vegetation within the class *Festuco-Brometea*. Their argument, based on similarity of species composition with dry grasslands, extends an old debate about the importance of vegetation physiognomy for its classification (e.g. Flahaut & Schröter 1910, Pignatti et al. 1995). Another disputable issue is different syntaxonomic treatments of fringe vegetation west and east of the Urals Mts (Yamalov & Kucherova 2009), which we address in the Discussion. We believe these inconsistencies may be alleviated by additional studies of forest-steppe structure and dynamics, and also by synthetic studies comparing composition and habitat requirements of fringe vegetation across large areas. Moreover, harmonization of criteria used for the delimitation of fringe vegetation, particularly against dry grasslands, is needed.

Here we provide new data and interpretations regarding fringe vegetation in the peri-Carpathian region of Western Ukraine and adjacent parts of Romania. Specific character of steppe vegetation in this region was recognized rather early (e.g. Procopianu-Procopovici 1882, Rudolph 1911, Koczwara 1927, 1931, Kozłowska 1930, Wierdak 1932). However its syntaxonomic grasp was hindered during Soviet times, when dominance-based approach to vegetation classification prevailed in the Ukraine (Didukh 2017), and modern syntaxonomic studies appeared only in the 1990s (Kukovitsia et al. 1994, 1998). Until now, some vegetation types have not received sufficient attention. Particularly the more mesic steppe communities, including the herb-dominated vegetation, lack satisfactory syntaxonomic treatment (Roleček et al. 2019a, 2019b). For example, *Trifolio-Geranietea* class is absent in the vegetation scheme of sinkholes published by Didukh & Pavliuk (2008) for Pokutia-Podnistrovia region (Western Ukraine), although it is

well developed there. Interestingly, already van Gils & Kozłowska (1977) anticipated that the Volyn-Podolian Upland (extending to our study area) should be a main distribution centre for the species from *Geranium sanguineum* group, which is characteristic for herb-rich fringes and steppe meadows.

During our field research in Western Ukraine we noticed that tall herb-rich vegetation often dominated by *Laserpitium latifolium* regularly develops on the most mesic and nutrient rich sites within steppe meadows. Some relatively moisture-demanding species (e.g. *Aegopodium podagraria*, *Cirsium erisithales*, *Galium mollugo* agg., *Gladiolus imbricatus*, *Lilium martagon*, *Veratrum lobelianum*, *Thalictrum aquilegiifolium*, *Trollius europaeus*) and heliophilous species with disjunct distributional ranges (e.g. *Actaea europaea*, *Adenophora liliifolia*, *Crepis sibirica*, *Ligularia glauca*) frequently participate in this community. While recent Ukrainian vegetation survey (Dubyna & Dzyuba 2019) does not include any corresponding syntaxon, similar vegetation was included in the Romanian national survey under the name *Clematis recti-Laserpitietum latifolii* Schneider-Binder 1984 (Coldea 2012).

Here we present new phytosociological data on the tall herb-rich vegetation from the peri-Carpathian region of Ukraine and adjacent part of Romania, compare it with previously published data, discuss position of the distinguished vegetation type in broad ecological and biogeographical context and suggest its syntaxonomic treatment respecting both its physiognomy and species composition. We also discuss suitable conservation management options.

Study area

Our study area includes margins of the Eastern Carpathian Mts and adjacent regions in the Western Ukraine and Romania. We use the designation "peri-Carpathian" (analogous to perialpine) for this area. Our vegetation plots come from the Bukovinian Pre-Carpathians, Pokutian-Bessarabian Upland (also called Moldavian Plateau) and Volyn-Podolian Upland north and east of the Eastern Carpathians, and the Transylvanian Basin south of the Eastern Carpathians (Fig. 1). Published data used for comparison come from broader region including Eastern Carpathians, Transcarpathian Ukraine, Slovakia and eastern half of Poland.

Climate of sampling sites is rather uniform. Mean annual temperature ranges between 8.0 and 9.0 °C and precipitation between 640 and 800 mm (CHELSA 1.2 dataset; Karger et al. 2017). This is a temperate continental climate (Rivas-Martínez et al. 2004), i.e. essentially a forest climate, supporting growth of broadleaved forests on zonal sites. Climatic variation is mainly due to elevation (220–550 m a.s.l.; some published stands in the Eastern

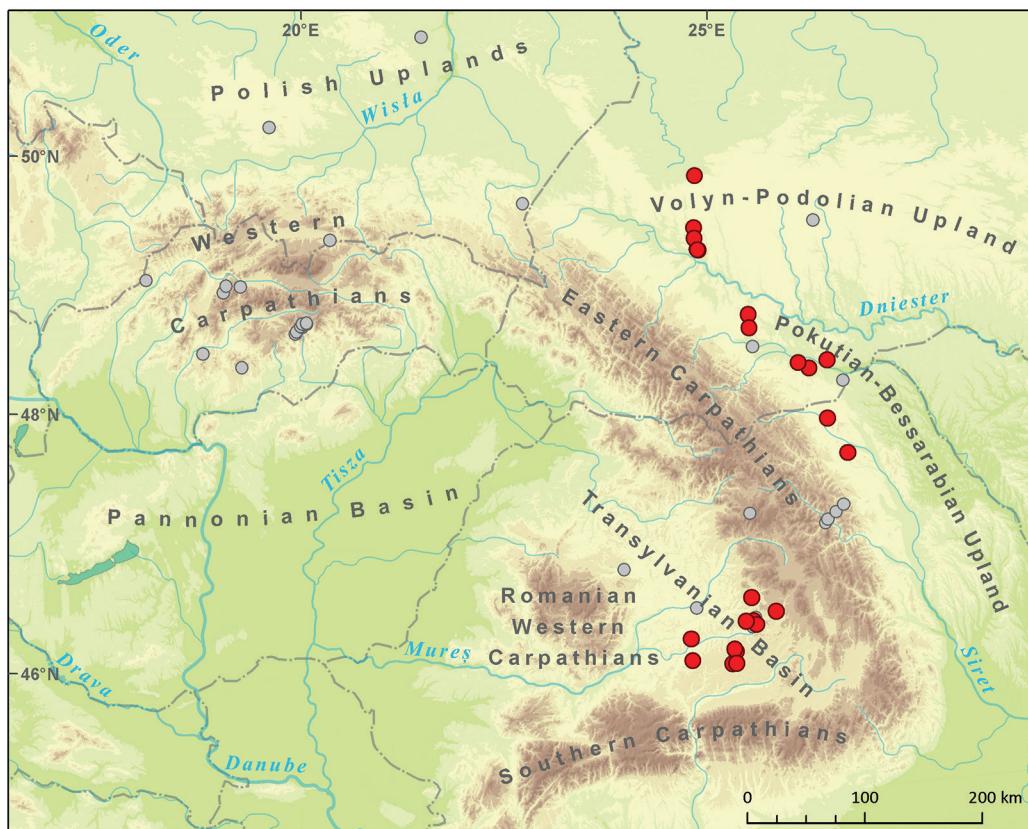


Fig. 1. Map of the study area. Distribution of *Trollio-Clematidetum recti* association according to the consensus classification in red. Relevés classified to clusters corresponding to this association by one or two algorithms in grey (a single relevé from northern Poland not shown).

Carpathians may reach up to 1000 m a.s.l.). On the other hand, generally higher elevation of Transylvania compensates for its more southern position.

Soils are mostly base-rich, formed over calcareous sedimentary bedrock. In Western Ukraine, most sampling sites (Fig. 2) were situated over Neogene gypsum (Chortova hora near Rohatyn, Kasova hora near Halych, Chortovets-Zalomy), other Neogene sediments (Dziurkach, Pidokruh and Boiany near Chernivtsi, Sinozhati and Velika Lysyna near Hvizdets, Dubrava near Yunashkiv) and Cretaceous calcareous sediments (Lysa hora near Zolochiv) (Shramenko 1969, Vashchenko et al. 2008). All newly sampled sites in Romania (Fânațele seculare de la Calafindești, Fânațele seculare Ponoare, glimée hills south of Apold) are situated over Neogene calcareous sediments (Geological Institute of Romania 2018). Landslides and other kinds of slope movements are a common feature across the study sites.

Methods

Data collection

We performed a field research of tall herb-rich vegetation in Western Ukraine and Romania between 2008 and 2019. It was focused on well-preserved steppe grasslands, often protected as nature reserves. Within the sites, we sampled places with maximum cover of herbs and maximum herb layer height, with species composition corresponding to the classes *Trifolio-Geranietea* and *Festuco-Brometea* (ruderal vegetation was avoided). We collected about 130 relevés which we databased using MS Excel and Turboveg for Windows 2.0 (Hennekens & Schaminée 2001). Besides species composition, basic data on habitat conditions (slope aspect and inclination) were collected for the relevés. For some relevés, finer data on stand structure (mean and maximum stand height) were measured and a mixed soil sample for pH and conductivity measurement was also taken in four places of each relevé from the uppermost 15 cm of soil profile. For further treatment of compositional data we used Juice 7.1 software (Tichý 2002). We restricted our dataset to tall herb-rich relevés using following criteria: summed cover of tall herbs



Fig. 2. Photos of some study sites: a) Kasova hora (Ukraine); b) Chortova hora (Ukraine); c) Chortovets-Zalomy site (Ukraine), June aspect with *Laserpitium latifolium*; d) Chortovets-Zalomy site (Ukraine), July aspect with *Veratrum nigrum* and *Actaea europaea*; e) Fânațele seculare de la Calafindești (Eastern Romania); f) glimée hills south of Apold village (Transylvania, Romania); g) traditional mowing of tall herb-rich steppe; h) traces of intentional fire ignition in the burned tall herb-rich steppe.

higher than 50% and percentage cover of other species (low herbs, graminoids, lianas) lower than 80%. Tall herbs were defined as herbs with mean height equal to or higher than 50 cm according to Kubát et al. (2002). For species not included in the latter reference values for closely related and morphologically similar species were used where available. For simplicity, grass-dominated relevés were considered as dry grasslands (class *Festuco-Brometea*) even if their species composition was similar to tall herb-dominated relevés (this pertained mainly to some *Brachypodium pinnatum*, *Calamagrostis arundinacea* and *Molinia arundinacea*-dominated grasslands). We complemented this dataset with 25 published relevés of the associations *Trollio-Clematidetum recti* and *Clematido-recti-Laserpitietum latifolii* retrieved from the Romanian literature (Täuber & Weber 1976, Schneider-Binder 1984, 2017, Schneider 1996).

For broader comparison we used 1049 relevés of the class *Trifolio-Geranietea* provided from the Polish (Kącki & Śliwiński 2012; 547 relevés), Romanian (Vassilev et al. 2018; 129 relevés) and Slovak (Šibík 2012; 373 relevés) national vegetation databases. We again restricted the dataset to relevés of tall herb-dominated vegetation, but also some low herbs, low shrubs and lianas considered diagnostic for the class *Trifolio-Geranietea* (*Fragaria moschata*, *Geranium sanguineum*, *Melampyrum cristatum*, *M. nemorosum* agg., *M. pratense*, *Polygonatum odoratum*, *Rosa gallica*, *Trifolium alpestre*, *T. medium*, *Vicia dumetorum*, *V. sylvatica*) were included to the sum of tall herbs to provide broader context for the studied vegetation. For Poland, only data from the eastern half of the country (east of 18.5°E) were used. The resulting dataset consisted of 711 relevés.

Data processing and analysis

We harmonized taxonomical concepts and nomenclature of vascular plants according to Euro+Med (2021) (exceptions are listed in Supplement S1). All records of woody species in the tree and shrub layers and the records of bryophytes were deleted. Also the records of vascular plant species that were not identified to species level were

deleted unless considered informative at the genus level (*Alchemilla*, *Crataegus*, *Rosa*, *Taraxacum*).

To put our newly sampled relevés of tall herb-rich vegetation into broader geographical and ecological context, we performed several classification and ordination analyses. Because pilot analyses indicated that the newly sampled relevés show high similarity to the associations *Trollio-Clematidetum* and *Clematido-Laserpitietum* described from Transylvania, our goal was to find all relevés that can be assigned to these associations. We used a less common classification strategy, which we call consensus classification: we performed several classification analyses using several commonly applied algorithms and interpreted the resulting clusters syntaxonomically based on diagnostic, constant and dominant species. The classifications were interpreted at the level of 10 clusters (i.e. the minimum expected number of associations in the study area). Relevés that were classified to the same cluster as type relevés of *Trollio-Clematidetum* and *Clematido-Laserpitietum* by all three classification algorithms were identified with these associations. The involved classification algorithms were: modified beta-flexible clustering ($\beta = -0.25$), K-means clustering, and TWINSPLAN algorithm modified according to Roleček et al. (2009). Percentage species abundances were square root-transformed (beta-flexible, K-means) or three pseudospecies cut levels (0, 2, 25%; Hill & Šmilauer 2005) were used (modified TWINSPLAN).

To evaluate compositional relationships between the clusters, we used non-metric multidimensional scaling from R library vegan (version 2.0-10; Oksanen et al. 2015) in R program (version 2.9.1, <http://www.R-project.org/> [last accessed 30 November 2020]) operated from JUICE, with square root transformation of percentage covers and down-weighting of rare species. To assist ecological interpretation of the results, mean ecological indicator values and mean plant heights were projected on the ordination space. Indicator values were adopted from Didukh (2011) as follows: Light = L_c ; Temperature = T_m ; Soil moisture = H_d ; Soil nitrogen = N_t ; Soil alkalinity = R_c . Mean values unweighted by cover were calculated from all species values in the plot. Diagnostic species of vegetation types were identified using the phi coefficient standardized to group size equal to 10% of the whole dataset (Tichý & Chytrý 2006) in JUICE. Species with phi value below 0.4 and species with a non-significant diagnostic value based on Fisher's exact test ($\alpha = 0.001$) were excluded.

Soil pH and conductivity (a proxy of mineral richness, especially calcium) were measured in distilled water suspension of soil sample (2:5) by a portable device (GMH Greisinger).

Results

Altogether 58 relevés (of them 20 new and unpublished elsewhere, see Supplement S2) were classified by all three classification algorithms to a cluster, whose diagnostic, constant and dominant species corresponded to the associations *Trollio-Clematidetum recti* Täuber et Weber 1976 and *Clematido recti-Laserpitietum latifoli* Schneider-Binder 1984. Type relevés of both associations were classified to the same cluster. Because *Trollio-Clematidetum* is a validly published, oldest and therefore correct name for this association (Roleček et al. 2019a), we identify our cluster with it. Further 58 relevés were classified to this cluster by one or two algorithms. Diagnostic (phi $\times 100 > 40$), constant (frequency $> 50\%$) and dominant (cover $> 10\%$ with frequency $> 10\%$) species of the association are the following:

Diagnostic species: *Euphorbia angulata* 69.3, *Clematis recta* 68.8, *Laserpitium latifolium* 67.7, *Sanguisorba officinalis* 60.6, *Helleborus purpurascens* 60.3, *Ferulago sylvatica* 50.3, *Veratrum nigrum* 48.9, *Ranunculus breyninus* 47.4, *Thalictrum aquilegiifolium* 46.5, *Mercurialis ovata* 45.8, *Tanacetum corymbosum* 45.7, *Potentilla alba* 44.6, *Lilium martagon* 43.9, *Filipendula vulgaris* 43.4, *Onobrychis viciifolia* agg. 43.0, *Carex montana* 41.8, *Trollius europaeus* 41.6.

Constant species: *Laserpitium latifolium* 88, *Dactylis glomerata* 78, *Clematis recta* 72, *Primula veris* 71, *Filipendula vulgaris* 64, *Tanacetum corymbosum* 64, *Brachypodium pinnatum* 62, *Elytrigia intermedia* agg. 60, *Vicia cracca* agg. 60, *Anthericum ramosum* 59, *Briza media* 59, *Euphorbia angulata* 59, *Ranunculus polyanthemos* agg. 57, *Salvia pratensis* 55, *Peucedanum oreoselinum* 53, *Polygonatum odoratum* 53, *Stachys officinalis* 53, *Trifolium alpestre* 53.

Dominant species: *Laserpitium latifolium* 67, *Clematis recta* 31, *Brachypodium pinnatum* 19, *Peucedanum oreoselinum* 16, *Briza media* 12, *Elytrigia intermedia* agg. 10.

Trollio-Clematidetum recti occurs on calcareous bedrock (gypsum, calcareous marlstone) with high soil pH (mean = 6.9; n = 9) and high soil mineral richness (mean conductivity = 518 µS/cm; n = 9). It prefers steep northern and north-western slopes (Fig. 3), although it may occur also in flat depressions and even on plateaus. Such habitats are productive, resulting in high stand height, both median (mean = 82 cm; n = 15) and maximum (mean = 176 cm; n = 14). Cover-weighted mean stand heights estimated from species composition are also high (mean = 77 cm; n = 58) and, among the analysed communities, comparable only to lianas-dominated vegetation classified to the alliance *Trifolion medi*. Position of the association in the context of K-means classification, whose results were the closest to the consensus classification, is shown in a NMDS plot (Fig. 4). Based on the division suggested by modified Twinspan, we distinguish two geographical variants of the association (Table 1). Variant with *Helleborus purpurascens* is distributed in Transylvania, variant with *Pulmonaria mollis* agg. in Ukraine and Romania east of the Carpathians.

Discussion

The concept of tall herb-rich steppe

Our results show that tall herb-rich vegetation is a widespread, though often small-scale component of forest-steppe mosaics in the peri-Carpathian region and its species composition is consistent across large area. The analysed stands in the Western Ukraine and Eastern Romania may be identified with the association *Trollio-Clematidetum*

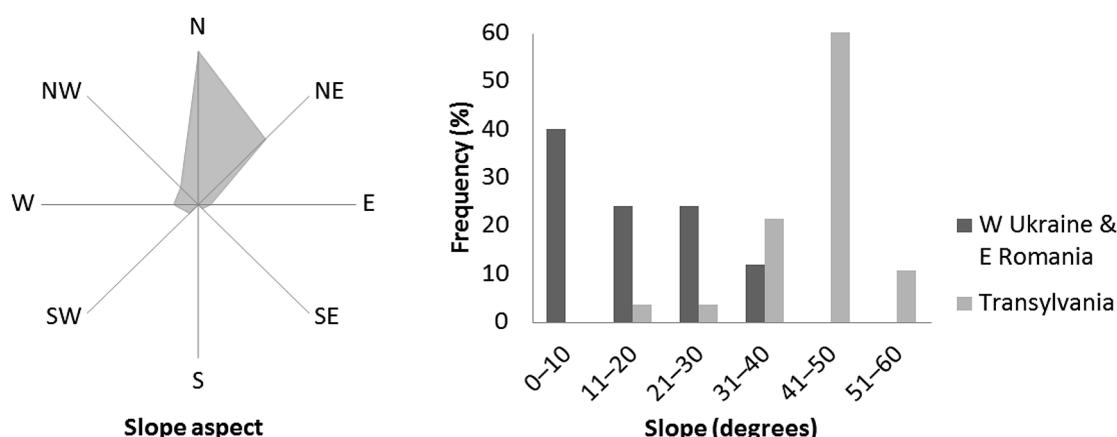


Fig. 3. Preferences of *Trollio-Clematidetum recti* for slope aspect (left) and slope inclination (right).

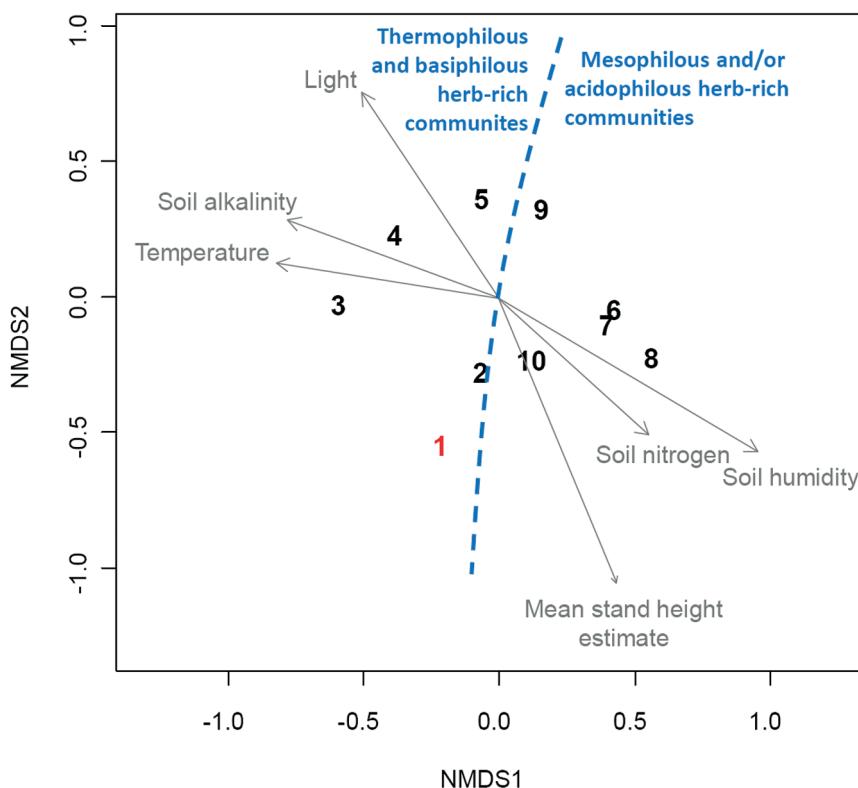


Fig. 4. NMDS plot showing the relationship between the association *Trollio-Clematidetum recti* and other types of fringe vegetation in East-Central Europe. Numerals are centroids of vegetation types distinguished by K-means clustering. Vectors of mean plant height and ecological indicator values are in grey. Legend: 1 – *Trollio-Clematidetum recti*; 2 – *Melampyrum nemorosum-Brachypodium pinnatum* community, 3 – *Teucrium chamaedrys-Geranium sanguineum* community, 4 – *Veronica incana-Anthericum ramosum* community, 5 – *Fragaria viridis-Seseli libanotis* community, 6 – *Hypericum maculatum-Trifolium medium* community, 7 – *Viola riviniana-Melampyrum nemorosum* community, 8 – *Galium odoratum-Vicia sylvatica* community, 9 – *Securigera varia-Festuca rubra* community, 10 – *Cirsium erisithales-Origanum vulgare* community. Diagnostic, constant and dominant species of the vegetation types are provided in Supplement S3.

tum recti (class *Trifolio-Geranietea*), described earlier from Transylvania. This vegetation usually occurs within larger tracts of steppe grasslands on calcareous soils, in concave parts of northern and north-eastern slopes and in depressions with deep soils such as sinkhole bottoms. The latter habitat is more common in the Ukraine, while very steep northern slopes of hillocks formed by specific kind of slope movement (slumping; Schneider 1996, Pop 2015) are a most frequent habitat in Transylvania.

We suggest that this tall herb-dominated vegetation rich in steppe elements is a specific steppe type, confined to relatively moist and nutrient rich sites. In contrast, its understanding as a forests fringe community dependent on forest may be misleading. It frequently occurs within large grassland tracts and can be maintained in treeless state for a long time (old maps suggest at least several hundreds of years). Also the regular occurrence of rather hygrophilous light-demanding species, which are absent or rare in the surrounding landscape, supports this idea. We assume that presence of forest species and the similarity with some communities of forest margins and open

canopy forests may result not only from the origin of these communities through deforestation (Koczwara 1931), but also from similar habitat conditions (shading by tall herbs, elevated air humidity in closed stands, low intensity of disturbance) and shared species pool.

Syntaxonomy

Both classification and ordination analyses and the analysis of diagnostic species support the treatment of *Trollio-Clematidetum recti* as a separate association identical with *Clematido recti-Laserpitietum latifolii* (the latter being a younger synonym). Although we identified quite many differential species for the stands in Western Ukraine, we assume that the concept of a broad association with shared dominant species (see e.g. Dengler & Boch 2008) may be applied here. Nevertheless, we refrain from formal syntaxonomic description of the geographical variants as subassociations, because we expect that further research may bring new information important

Table 1. Geographical variants of the association *Trollio-Clematidetum recti* as suggested by modified Twinspan algorithm. Percentage frequencies of differential species (phi > 0.40; Fisher's exact test alpha = 0.001; frequency values in bold) and other frequent species (sorted by mean frequency) are shown.

	Variant <i>Pulmonaria mollis</i> agg. Frequency [%] n = 25	Variant <i>Helleborus purpurascens</i> Frequency [%] n = 33
Differential species		
<i>Pulmonaria mollis</i> agg.	80	0
<i>Calamagrostis arundinacea</i>	44	0
<i>Molinia caerulea</i> agg.	32	0
<i>Trifolium pannonicum</i>	52	3
<i>Serratula tinctoria</i>	60	6
<i>Bromopsis inermis</i>	40	3
<i>Helleborus purpurascens</i>	0	76
<i>Onobrychis viciifolia</i> agg.	0	61
<i>Seseli annuum</i>	0	33
<i>Pimpinella saxifraga</i> agg.	0	33
<i>Festuca rubra</i> agg.	4	45
Other frequent species		
<i>Laserpitium latifolium</i>	80	94
<i>Dactylis glomerata</i>	68	85
<i>Primula veris</i>	88	58
<i>Clematis recta</i>	44	94
<i>Tanacetum corymbosum</i>	84	48
<i>Filipendula vulgaris</i>	72	58
<i>Brachypodium pinnatum</i>	80	48
<i>Vicia cracca</i> agg.	80	45
<i>Elytrigia intermedia</i> agg.	64	58
<i>Euphorbia angulata</i>	60	58
<i>Anthericum ramosum</i>	56	61
<i>Ranunculus polyanthemos</i> agg.	48	64
<i>Stachys officinalis</i>	64	45
<i>Briza media</i>	24	85
<i>Peucedanum oreoselinum</i>	52	55
<i>Salvia pratensis</i>	40	67
<i>Sanguisorba officinalis</i>	80	24
<i>Polygonatum odoratum</i>	40	64
<i>Trifolium alpestre</i>	40	64
<i>Cruciata glabra</i>	60	42
<i>Carex montana</i>	56	39
<i>Trifolium montanum</i>	36	55
<i>Geranium sanguineum</i>	60	27

for their syntaxonomic treatment. We also remark that according to our observations, the differences in management (abandonment-burning versus grazing-mowing) may deepen the geographical differentiation between the two variants.

The number of relevés assigned to this association by a single or two classification algorithms is not negligible (58 relevés). Further research is needed to show whether more types of tall herb-rich steppe can be distinguished in the study area or whether these relevés represent just less characteristic stands either formed by broadly distributed species or transitional to other vegetation types.

Classification of *Trollio-Clematidetum* at the alliance level is not a trivial one. Presence of many steppe species supports assignment to the *Geranion sanguinei* alliance, in agreement with the latest Romanian vegetation survey (Coldea 2012). However, *Trollio-Clematidetum* avoids warm and dry sites and is differentiated from many other *Geranion sanguinei* communities by high frequency of relatively hygrophilous and cold-tolerant (even montane) species such as *Dactylis glomerata*, *Ranunculus breyninus*, *Sanguisorba officinalis* and *Trollius europaeus*. In this respect the association resembles another *Laserpitium latifolium*-dominated association, *Trifolio-Laserpitietum latifolii* van Gils & Gilissen 1976, described from the continental part of the Central Alps. The latter has been classified by some authors (e.g. Mucina & Kolbek 1993) to the mesophilous alliance *Trifolion medii*, while van Gils & Gilissen (1976) suggested that it may deserve a separate suballiance within the *Geranion sanguinei* alliance (which they named *Trifolio-Geraniencion sanguinei*), together with some other relatively mesophilous fringe communities of subboreal Europe. The latter are nowadays classified within a separate alliance *Galio littoralis-Geranion sanguinei* Géhu et Géhu-Franck in de Foucault et al. 1983 (Mucina et al. 2016), but Dengler & Boch (2008) suggested that *Laserpitium latifolium*-dominated stands in subboreal regions might be rather classified within the *Geranion sanguinei*. To conclude from this entangled issue, we suggest keeping things simple and continuing classification of *Trollio-Clematidetum* within the *Geranion sanguinei* alliance. If finer division is needed, a separate suballiance *Trifolio-Geraniencion sanguinei* may be considered.

Besides relationships within the *Trifolio-Geranietea* class, similarities with some tall herb-dominated communities of high elevations, classified to the class *Mulgedio-Aconitetea*, deserve attention. Particularly *Anemono narcissiflorae-Laserpitietum latifolii* Grebenščíkov et al. 1956 and *Convallario majalis-Calamagrostietum variae* (Sillinger 1933) Kliment et al. 2004, reported from Slovak Western Carpathians (Kliment & Valachovič 2007), share many species (e.g. *Adenophora liliifolia*, *Anemonastrum narcissiflorum*, *Anthericum ramosum*, *Astrantia major*, *Brachypodium pinnatum*, *Bupleurum falcatum*, *Calamagrostis arundinacea*, *Cirsium erisithales*, *Convallaria ma-*

jalis, *Dactylis glomerata*, *Laserpitium latifolium*, *Lilium martagon*, *Polygonatum odoratum*, *Ranunculus breyninus*). Conversely, tall herb-rich steppe and related communities in northernmost Podolia (Holohory hills) include more dealpine elements than elsewhere in Ukraine, e.g. *Calamagrostis varia*, *Carduus defloratus* and *Coronilla coronata*. We assume that this phenomenon points to historical interconnection between the steppic and sub-alpine treeless habitats (Roleček et al. 2015). It provides further support for the hypothesis that these vegetation types are linked to the once widespread Pleistocene and early-Holocene hemiboreal and montane forest-steppe (Kagalo 1990, Roleček et al. 2014).

Analogues across Europe and Western Siberia

Analogues of the peri-Carpathian tall herb-rich steppe can be found across temperate Eurasia. They occur mainly in the regions with base-rich soils and sufficient precipitation, supporting the growth of shady forests, as well as productive non-forest vegetation (van Gils & Keysers 1976). At the same time, connectedness to sources of heliophilous steppe species is required. These species may have persisted here either due to site heterogeneity (e.g. on steep sunny slopes with rock outcrops and screes) or may have spread from adjacent steppe regions or may have been preserved due to a long-term disturbance regime. Such conditions are usually met on mountain peripheries and in intermontane basins in the (sub)continental parts of Eurasia. Similar communities have been preserved also in the hemiboreal zone (Dierschke 1974, Diekmann 1997, Dengler & Boch 2008, Iakushenko 2017), where the precipitation sums are usually lower, but lower temperatures reduce the demands for moisture.

Peripheries and continental regions of the Alps (Gradmann 1898, Müller 1962, van Gils & Gilissen 1976), the Carpathians (Rudolph 1911, van Gils & Kovács 1977) and the Balkan mountain ranges (van Gils et al. 1975) harbour well-developed tall herb-rich vegetation. However, numbers of continental steppe species are inevitably lower in the Alps and the Balkans, while alpine and sub-Mediterranean element is more represented. As a result, the term steppe was little used in connection with herb-rich vegetation in these regions (but see Gradmann 1898, Müller 1962) and its similarity with the communities discussed here may have been underestimated. On the other hand, the Carpathians border on the continental forest-steppe belt and the steppe element is well represented here, particularly on the contact with the Pannonian basin, Transylvanian basin and along the outer margin of the Southern and Eastern Carpathians (where also our study area extends). In higher elevations of the mountain range, and also in Polish Uplands, the number of steppe species is lower, which is likely the main reason why tall



Fig. 5. Tall herb-rich steppe dominated by *Seseli libanotis* and *Phlomis tuberosa* has developed as a post-fire successional stage on Shaytan-Tau ridge (South Urals Mts).

herb-rich communities in these regions were not classified to *Trollio-Clematidetum*.

The next area to the east where the forest-steppe belt is intersected by the mountains is South Urals Mts (leaving aside the Caucasus region, for which few relevant data are available; Demina et al. 2017, Tsepko 2019). Herb-rich vegetation is broadly distributed and rather well-studied in the South Urals region (Yamalov & Kucherova 2009, Yamalov et al. 2012, Korolyuk et al. 2016), although its assignment to *Trifolio-Geranietaea* versus *Festuco-Brometea* class may require revision. Nevertheless, tall herb-rich steppe dominated e.g. by *Seseli libanotis* undoubtedly thrives here on forest fringes, glades and in post-fire successional stages (Fig. 5). It shares many species with open-canopy forests dominated by oak, birch and pine (Chytrý et al. 2010).

East of the Urals, and especially in the mountains in the south of Western Siberia, where shading broad-leaved trees are almost absent due to continental climate, a large diversity of *Trifolio-Geranietaea* communities might be expected. Indeed, herb-rich steppe meadows and tall herb-dominated vegetation are abundant here. However, their syntaxonomic concept is quite different from the European ones and they are classified within mesic and wet meadows (*Molinio-Arrhenatheretea*) as a separate order *Carici macrourae-Crepidetalia sibiricae* (Mucina et al. 2016). From the Central European point of view, it is a heterogeneous order that mixes semi-dry, mesic and

slightly wet grasslands and herb-dominated stands. Its species composition is closely linked to the herb layer of open hemiboreal forests of the class *Brachypodio pinnati-Betuletea pendulae* (Ermakov et al. 1999, Ermakov et al. 2000, Korolyuk et al. 2016). They are called “forest meadows” and besides natural forest-steppe mosaics, they occur on forest margins and glades used for hay production and grazing or in successional stages following fire, frost damage or logging (Ermakov et al. 1999). The co-occurrence of forest-steppe and montane elements, which we observed in *Trollio-Clematidetum*, is a common feature of these communities, especially their xerophilous alliance *Aconito barbati-Vicion unijugae* Ermakov et al. 1999. They also share many characteristic species with Central European tall herb-dominated vegetation (or their close relatives), such as *Aconitum lycoctonum*, *Actaea cimicifuga* L., *Brachypodium pinnatum*, *Crepis sibirica*, *Euphorbia pilosa* L., *Lathyrus pisiformis*, *Ligularia glauca*, *Lilium martagon* var. *pilosiusculum*, *Pulmonaria mollis* agg., *Sanguisorba officinalis*, *Trollius asiaticus* and *Vicia cracca* agg. We suggest that vegetation complexes of *Trollio-Clematidetum* and herb-rich semi-dry grasslands (alliance *Cirsio-Brachypodion pinnati*) in the peri-Carpathian region are direct analogues of the complexes of forest meadows and meadow steppes (e.g. alliance *Aconito barbati-Poion transbaicaliae*; Korolyuk & Makunina 2001) in the Altai-Sayan region, despite the fact that they are separated by more than

4000 km. This similarity is probably given not only by similar habitat conditions and climate (leaving aside the obvious differences in continentality, the summer temperatures and precipitation sums are similar), but also by their common history, particularly the link to Pleistocene-early Holocene pine- and birch-dominated forest-steppe. While in Central Europe their distribution has been greatly reduced, probably mainly due to the expansion of shady broad-leaved forests during the Holocene (Hájková et al. 2011, Pokorný et al. 2015), east of the Urals their diversity has been preserved either in the continental forest-steppe mosaics or in the extremely species rich open-canopy forests (Chytrý et al. 2012).

Dynamics and conservation management

Similarly to other vegetation types growing in favourable habitat conditions (Galvánek & Lepš 2012), tall-forb steppe is subject to successional development in the absence of management. We observed accumulation of biomass, spread of competitive species (e.g. *Chaerophyllum bulbosum*, *Phragmites australis*, *Pteridium aquilinum*, *Rubus* sp. div., *Sambucus ebulus*), shrub and tree encroachment. We assume that most successional pathways on these sites tend towards mesophilous broad-leaved forests of *Carpino-Fagetea sylvaticae* class (Fig. 6).

The assumed long-term stability of tall-herb steppe therefore requires regular disturbances. We have observed grazing and mowing in several sites (mainly in Romania), while many sites in Ukraine showed some degree of abandonment or traces of spring burning. We suppose that with increasing grazing and mowing pressure, tall herb-rich communities are replaced by grasslands. Their species composition is particularly similar to semi-dry grasslands related to the *Brachypodio pinnati-Molinietum arundinaceae* association (Roleček et al. 2019, Willner et al. 2019) and some authors (e.g. Koczwar 1931) even treated them as a single community. The latter author also observed retreat of steppic species following too intensive mowing, grazing and other disturbances (plowing, digging). They were replaced by mesophilous or drought tolerant grasses (mainly *Agrostis*, *Briza media*, *Elytrigia intermedia* and *Schedonorus pratensis*). We assume that such stands may develop towards mesic grasslands of the *Arrhenatherion elatioris* alliance, especially where fertilizers have been applied (Roleček et al. 2015). This dependence on management regime may be one of the reasons why this species-rich community with characteristic species composition has not been distinguished in many studies.

Many sites abandoned in the last decades have preserved their species-rich steppe vegetation thanks to the regular early spring burning (Fig. 2), which prevents ac-

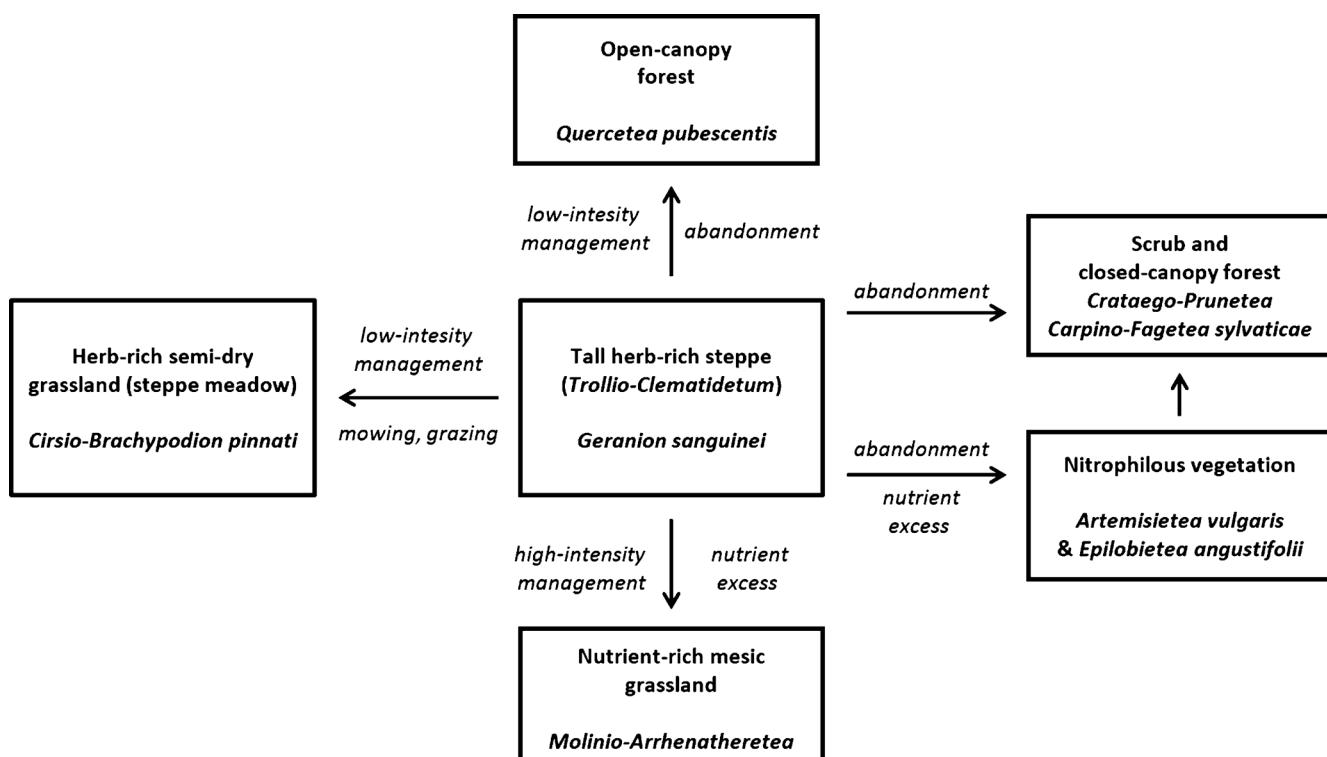


Fig. 6. Concept of successional status of tall herb-rich steppe.

cumulation of dead biomass and encroachment of woody species. While some adverse effects of burning on steppe plants and other biota have been reported (Ryser et al. 1995, Nemkov & Sapiga 2010), it has a vital role in maintaining the open or semi-open character of abandoned forest-steppe habitats (Peterson & Reich 2008, Ónodi et al. 2021). Moreover, we assume that nutrients retained in the soil following burning may support tall herbs, while mowing or grazing may suppress them. We therefore recommend prescribed burning as a simple and cheap management option for tall herb-rich steppe sites where mowing or low-intensity grazing are unavailable, impractical or where other measures do not seem to support the desired condition. Further research on the effects of mowing, grazing, burning and their combinations on the biodiversity of east-central European steppes is also needed.

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Supplement S1: The taxonomical concepts and nomenclature of vascular plants used in the text and deviating from Euro+Med PlantBase (<http://ww2.bgbm.org/EuroPlusMed>) or not included therein.

Supplement S2: New relevés of *Trollio-Clematidetum* association from Ukraine and Romania.

Supplement S3: Diagnostic, constant and dominant species of 10 types of herb-rich vegetation distinguished by K-means clustering.

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