

Chalk rocky grasslands in the arid Eastern European Plain

Kalkfelsrasen in der trockenen osteuropäischen Tiefebene

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Abstract

Chalk rocky grasslands of the arid Eastern European Plain are endangered and highly important for biodiversity protection. This study aimed to revise previous syntaxonomic concepts, compare chalk rocky grasslands with other calcareous rocky grasslands and provide a unified classification of chalk rocky grasslands. We extracted relevés from the European Vegetation Archive and added relevés from protologues and papers describing chalk rocky grasslands within the study area. We pre-selected an initial dataset of calcareous rocky grasslands, which we narrowed down to the class *Stipo pulcherrimae-Festucetalia pallentis*. These were further classified using a modified TWINSpan algorithm. We classified them as *Anabasio cretaceae-Agropyrion desertori*, *Sileno fruticosae-Nanophytion erinacei*, *Anthemido trozkianae-Artemision salsoloides*, *Sileno supinae-Artemision hololeucae*, *Euphorbio cretophilae-Thymion cretacei* and transitional communities of the *Centaureo carbonatae-Koelerion talievii* alliances within two orders with validation of some syntaxa. The communities are clearly differentiated from each other along gradients of climate and edaphic properties. Differences to other European limestone communities are given. We provide the first unified European classification of continental chalk rocky grasslands, including Ukrainian, Russian and Kazakh communities.

Keywords: chalk rocky grasslands, vegetation, Eastern European Plain, Ukraine, Kazakhstan

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Chalk rocky grasslands dominated by specific endemic chamaephytes and hemi-cryptophytes with star-shaped and cobwebby pubescence occur in eastern Europe's chalk outcrops of river valleys. They occupy skeletal soils (rendzic, calcareous and calcic leptosols) and strongly depend on the high carbonate content of the chalk bedrock.

The vegetation of chalk outcrops has been studied since the late 19th century and has been the subject of numerous discussions, particularly regarding its classification, structure, and origin. Litvinov (1891, 1902) initially characterized chalk rocky grasslands. Later, Kozo-Polianskyi (1931) distinguished two components within it: the “hyssop flora” (*Hys-sopus cretaceus*, *Artemisia hololeuca*, *A. salsoloides*), which has a relict character and is genetically related to the southern flora of the Central and Middle Asia, and the flora of

“lower alpine” habitats, associated with northern Periglacial steppes (e.g. *Carex humilis*, *Androsace kozo-poljanskii*). Chalk rocky grasslands, unlike steppes dominated by hemi-cryptophytes with the high presence of graminoids, are characterized by a sparse cover (up to 60%) consisting mainly of chamaephytes, forming on skeletal soils without continuous dead litter. Taxonomically, many genera of *Thymus*, *Helianthemum*, *Artemisia*, *Hyssopus*, *Scrophularia*, *Pimpinella*, and *Asperula*) are subdivided into sections, subsections, series, and numerous “minor” vicarious species endemic to specific regions, indicating the uniqueness of this flora and progressive evolution of speciation (Lavrenko 1961). This distinctiveness from steppe vegetation was reflected in dominant classifications, with this vegetation being treated as thyme communities (Lavrenko 1961) or tomilliaries (Didukh 1981, 1989), analogues of Balkan phrygana.

A classification of the chalk rocky steppe vegetation of the Central Russian Upland (Ukraine and part of Russia) was first provided by Didukh (1989), who described a new order of *Thymo cretacei-Hyssopetalia cretacei* and lower syntaxa within the *Festuco-Brometea* class. Romashchenko et al. (1996) described chalk rocky vegetation within a new class of *Helianthemo-Thymetea* that was not floristically similar to pure steppe vegetation, in which the *Thymo cretacei-Hyssopetalia cretacei* order, *Artemisio hololeuca-Hyssopion cretacei*, *Euphorbio cretophilae-Thymion cretacei* and *Centaureo carbonatae-Koelerion talievii* alliances were considered. Further studies of chalk rocky vegetation in Ukraine and Russia have been analyzed in detail by Didukh et al. (2018); however, the similarity of chalk and limestone rocky grasslands led to misinterpretation in Moldova (Rushchuk et al. 2005, Pinzaru 2006).

Chalk rocky vegetation has also been described within *Anabasieta cretaceae* (Golovanov et al. 2021) east of the Volga River in the steppe region that transforms into a semi-desert and desert region in the south, which has specific desert-steppe, North Turanian steppe species (Darbaieva 2003, Riabinina & Lukianova 2005, Saksonov et al. 2019, Golovanov et al. 2021).

Generally, Mucina et al. (2016) consider these communities within the zonal steppe vegetation of the *Festuco-Brometea* class, which spreads along the temperate belt and varies from Mediterranean wet to Asian aridic conditions.

However, the absence of *Festuco-Brometea* diagnostic species causes a heated discussion about their modern syntaxonomy. The *Centaureo carbonatae-Koelerion talievii* alliance has been considered within the *Festucetalia valesiacae* or *Stipo pulcherrimae-Festucetalia pallentis* orders due to the floristic and ecological similarities of these communities with rocky grasslands (Mucina et al. 2016, Didukh et al. 2021).

Chalk rocky grasslands are currently endangered and highly important for biodiversity protection. The main threats are afforestation, terracing of the slopes and the mining of chalk and marl (Kuzemko 2022). Since the Russian aggression in 2014, new threats have arisen that influence the endangered chalk rocky grasslands: direct vanishing of the vegetation cover due to intensive military activities, abandoned agricultural lands near the slopes of chalk outcrops and proliferation of invasive species. Nevertheless, in the Bern Convention, they are of conservation importance in Europe as E1.13 Continental dry, rocky steppe grasslands and dwarf scrub on chalk outcrops (Schaminée et al. 2016).

The main goal of the current study was to revise the classification of chalk rocky vegetation within the Eastern European Plain based on a large international dataset, and to complete knowledge of its syntaxonomy, ecology and distribution. To achieve this goal, we aimed to (1) revise the syntaxonomy of chalk rocky vegetation within the Eastern European

Plain and compare it with other types of calcareous rocky grasslands; (2) analyse the distribution of chalk rocky grasslands within the study area; (3) characterise the main environmental factors that cause the differentiation of chalk rocky grasslands.

2. Study area

We considered rocky grasslands on chalk outcrops within the aridic zone of the Eastern European Plain (Fig. 1). Specifically, we focused on two distinct regions: (1) the Central Russian Upland, and (2) the Sub-Ural Upland across a climatic gradient that significantly impacts the distribution and composition of vegetation types within the study area in which chalk outcrops occur.

The Central Russian Upland occupies eastern Ukraine and southwestern Russian Federation, extending from northwest to southeast, from the right bank of the Oka to the Donets River, with an elevation of 230–250 m a.s.l. (Anon 2007). The Central Russian Upland is built of Precambrian deposits of the crystalline Voronezh Massif covered by layers of sedimentary deposits of the Devonian, Jurassic, Cretaceous and Paleogene periods (Anon 2007). The Central Russian Upland has a sub-continental (subaridic) climate, characterised by large temperature amplitudes between winter and summer. It generally has 450–500 mm annual precipitation, with an average temperature of around -4 – 6 °C in January and $+21$ – 24 °C in July, with essential temperature amplitudes (27 – 30 °C), Gorchinskyi continentality coefficient ($I_g = 42$ – 46), de Martonne coefficient of aridity-humidity ($I_{dm} = 28,5$ – 25), with a wetter climate in the western parts of the region and a drier climate in the east (Karger et al. 2017, Didukh 2023).

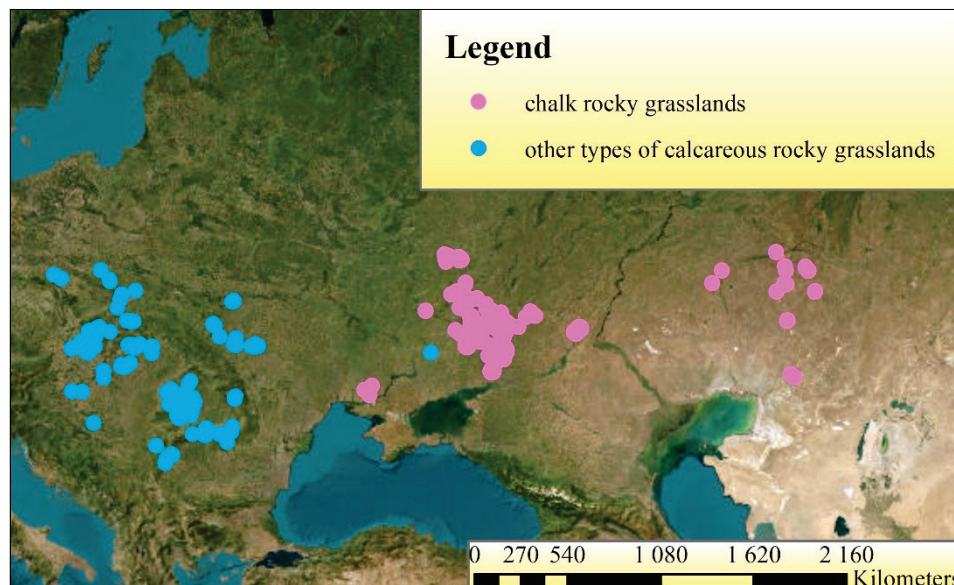


Fig. 1. Map of the chalk rocky grasslands compared with other types of calcareous rocky grasslands distribution.

Abb. 1. Karte der untersuchten Kalkfelsrasen im Vergleich zu anderen Typen von Kalkfelsrasen.

The Sub-Ural Upland is a geological and geographical region occupied by the Aktobe region in Kazakhstan, with a northwestern part in the West Kazakhstan Region and a small northern part in the Orenburg region (Russian Federation) with an elevation of 100–450 m a.s.l. (Anon. 2010). The Sub-Ural Upland predominantly comprises ancient crystalline rocks, including granite and gneiss, formed during the Precambrian period. It also contains upper layers of sedimentary bedrock, such as limestone, chalk and sandstone, deposited during later geological periods. The climate in the Sub-Ural Upland region varies depending on the location and elevation. Generally, it experiences a subcontinental climate with moderate annual precipitation, which typically ranges from 250 to 400 mm, with slightly higher amounts in the western parts of the upland, with an average temperature of around -9–13 °C in January and +22–25 °C in July, with essential temperature amplitudes (30–36 °C), Gorchinskyi continentality coefficient ($I_g = 46–60$), de Martonne coefficient of aridity-humidity ($I_{dm} = 25–20$) (Karger et al. 2017, Didukh 2023).

3. Materials and methods

3.1 Vegetation data for broad-scale comparison

To revise the high-level syntaxonomical units of chalk rocky vegetation, we digitised data from the literature or extracted it from EVA and used it for comparison with data from the study area and adjacent territories.

We selected the data from the literature with original diagnoses of the *Anabasietaea cretaceae* class Golovanov et al. 2021 (146 relevés), the “*Helianthemo-Thymetea* class Romashchenko et al. 1996” (225 relevés), the “*Thymo cretacei-Hyssopetalia cretacei* order Didukh 1989” (90 relevés) and subordinate syntaxa (181 relevés) (Sereda 2008, 2009, Demina 2011, Poluyanov & Averinova 2012, Averinova 2014, Koroliuk et al. 2021).

In the EVA database (Chytrý et al. 2016), we also selected all relevés of calcareous rocky grasslands from Poland (87 relevés), Slovakia (250 relevés), Hungary (751 relevés), Romania (357 relevés), Ukraine and Moldova (580 relevés) assigned to the *Stipo pulcherrimae-Festucetalia pallentis* order Pop 1968 or subordinate syntaxa, by the initial authors or custodians of the databases. Additionally, we created a database of the Central Russian Upland (504 relevés) and added it to the general dataset.

We unified the taxonomy of vascular plants according to Euro+Med Plantbase (Euro+Med 2006+) and, in addition, Cherepanov’s checklist (1995), bryophytes according to Hodgetts et al. (2020), and lichens according to the Index Fungorum (2021). We combined them into aggregates (Supplement E1), removed bryophytes and lichens because they were not recorded in some relevés, and returned them to the final synoptic table (Supplement E2).

3.2 Expert system processing

From the initial dataset of 3171 relevés, we selected relevés assigned as EUNIS habitats R1C, R15, R16 and R based on the EUNIS-ESy expert system (Chytrý et al. 2020). Afterwards, we checked these relevés by the expert system of Willner et al. (2017) and extracted data assigned to the *Stipo pulcherrimae-Festucetalia pallentis* order. Other relevés, such as other EUNIS habitat codes and *Festuco-Brometea* orders, were removed from the analysis. After expert processing, we got a dataset of 1643 relevés of the calcareous vegetation.

3.3 TWINSpan classification

In our analysis, we applied a modified TWINSpan algorithm (Hill 1979, Roleček et al. 2009), utilising three pseudospecies cut levels of 0%, 5% and 25% cover. The minimum group size for the division was set at five relevés, and Whittaker’s beta coefficient served as a metric for internal cluster

heterogeneity. We assessed the optimal number of clusters using OptimClass 1 (Tichý et al. 2010) on the first stage of the analysis.

On reviewing the classification results, we employed non-modified TWINSpan (Hill 1979) to classify three clusters separately, in view of their ecological and floristic heterogeneity. The same pseudospecies cut levels (0%, 5% and 25% cover) were used, with a minimum group size for division set at ten relevés and two division levels.

Diagnostic species for each cluster were identified based on the phi-coefficient of association and applied to virtually standardised cluster sizes (Chytrý et al. 2002, Tichý & Chytrý 2006). A fidelity threshold of $\phi = 0.30$ was used, together with Fisher's exact test ($p < 0.05$).

3.4 Ecological indicators and distribution of the communities

We used EIVE 1.0 scales (Dengler et al. 2023) to find environmental differences between main orders of calcareous rocky grasslands in the broad-scale comparison context.

In addition, we used Didukh's scales to explore environmental differences in chalk rocky grasslands within the study area precisely. The phytosociological scales of Didukh (2011) reflect amplitude indices of the species characterised by the following dimensions: ecological indicator of soil humidity (Hd – 23 grades), ecological indicator of variability of damping (fH – 11 grades), ecological indicator of soil acidity (Rc – 15 grades), ecological indicator of total salt regime (Sl – 19 grades), ecological indicator of carbonate content (Ca – 13 grades), ecological indicator of nitrogen content (Nt – 11 grades), ecological indicator of soil aeration (Ae – 15 grades), ecological indicator of thermoregime (Tm – 17 grades), ecological indicator of humidity of microclimate (Om – 23 grades), ecological indicator of continentality (Kn – 17 grades), ecological indicator of cryoregime (Cr – 15 grades) and ecological indicator of light in the community (Lc – 9 grades).

For each relevé, we calculated non-weighted means of species' values for the environmental parameters and fitted them to the Detrended Correspondence Analysis (DCA) ordination plot using *envfit* function of the *vegan* R package. DCA was also calculated using *vegan*, with default parameters. We transformed species abundance data from the seven-grade Braun-Blanquet cover-abundance scale to percentage covers as follows: r = <1%, + = <2%, 1 = <3%, 2 = 13%, 3 = 38%, 4 = 68%, 5 = 88%. The obtained values were then log-transformed as $\log(x + 1)$ to diminish distribution skewness (Borcard et al. 2018, Tichý et al. 2020).

Depending on anatomical and morphological features, physiological and biological properties, growth processes, plant development, preservation and transmission of genetic information, three ecological strategies were distinguished: CRS, which reflects assimilation, accumulation and transfer of resources, and energy. To define the strategies of species on the phytosociological level, we constructed a Grime's triangle using Didukh's methodology (Supplement E3).

Based on the predominance of the species strategy types in the communities, we considered three types of habitats: SPE (successive ecosystems), C – concurrent strategy PSE (persistent stable ecosystems), S – stress-tolerance strategy and FLE (fluctuation labile ecosystems), R – ruderal strategy (Didukh 2023). This approach makes it possible to evaluate the ecological strategy from the standpoint of functioning, specifics of development, dynamics and stability of ecosystems, in particular conditions of existence, which assimilate, accumulate and transfer resources and energy, and preserve and ensure the spread of genetic material (Didukh 2023).

In addition, we classified all the vascular plants into one of the Raunkiaer plant life forms: therophytes, geophytes, hemicryptophytes, chamaephytes and phanerophytes (Raunkiaer 1934). The data are available in Supplements E2.

3.5 Applications and Software

The results were visualized using *vegan* version 2.6-4 (Oksanen 2022) and *ggplot2* (Wickham 2016) packages in R (R Core Team 2021). The TWINSpan classification was done with JUICE version 7.1 (Tichý 2002). Maps were created using ArcGIS 10.8.2. We used the following sources as the basemaps: National Geographic World Map, World Imagery, Biomes and Ecoregions 2017 (<https://services.arcgis.com>).

4. Results and Discussion

4.1 Cluster results of the initial vegetation dataset

We obtained 8 clusters after the suggestion of Optimclass 1 (Tichý et al. 2010) using the modified TWINSpan algorithm (Roleček et al. 2009) in the first stage of the analysis. In the second stage of the analysis, we classified the first, second and last clusters separately due to the floristic heterogeneity of their constructions using the original TWINSpan algorithm (Hill 1979) and obtained thirteen clusters (Fig. 2). The first six clusters (also Table 1) that contained chalk rocky grasslands (482 relevés) are described in detail below. The 7–13 clusters (1161 relevés) corresponding to the order *Stipo pulcherrimae-Festucetalia pallentis* that is not in the scope of our paper and used for comparison of life forms and ecological strategies are shown in supplementary materials (Supplement E4).

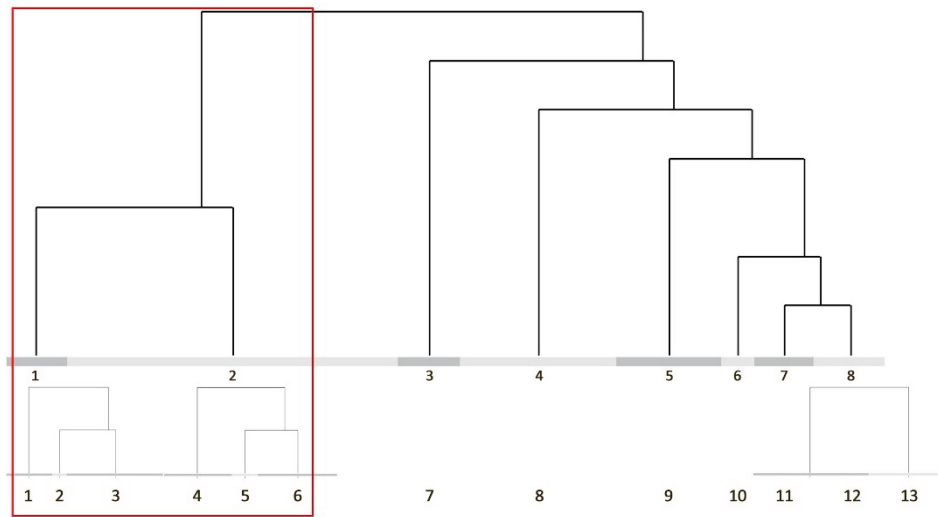


Fig. 2. Dendrogram of chalk rocky grasslands and other calcareous rocky grasslands based on the TWINSpan algorithm. The upper dendrogram represents the first stage (eight clusters were obtained), and the lower diagrams represent the second stage (thirteen clusters were obtained). The chalk rocky grasslands are highlighted with the red frame. Non-highlighted clusters represent the other types of calcareous rocky grasslands.

Abb. 2. Dendrogramm der untersuchten und anderen Kalkfelsrasen basierend auf dem TWINSpan-Algorithmus. Das obere Dendrogramm stellt die erste Stufe dar (es wurden acht Cluster erhalten), und die unteren Diagramme stellen die zweite Stufe dar (es wurden dreizehn Cluster erhalten). Die untersuchten Kalkfelsrasen sind mit einem roten Rahmen hervorgehoben, während die nicht hervorgehobenen Cluster die anderen Typen von Kalkfelsrasen darstellen.

Table 1. The shortened synoptic table shows the percentage constancy of species in six clusters that represent chalk rocky grasslands. Species are ranked by decreasing fidelity measured with the *phi*-coefficient, which is not shown. Species with a *phi*-value greater than 0.30 are considered diagnostic and shaded in light grey; species with a *phi*-value greater than 0.50 are considered highly diagnostic and shaded in dark grey. Species highly diagnostic or diagnostic in one cluster are accepted as diagnostic for alliances; species highly diagnostic or diagnostic in more than one cluster are accepted as diagnostic for high-rank syntaxa. Species with a constancy of 15% or less in individual columns are not shown in the table unless they are diagnostic.

Tabelle 1. Die gekürzte synoptische Tabelle zeigt die prozentuale Stetigkeit der Arten in sechs Clustern von Kalkfelsrasen. Die Arten sind nach abnehmender Treue geordnet, gemessen mit dem nicht angegebenen *phi*-Koeffizienten. Arten mit einem *phi*-Wert größer als 0,30 gelten als diagnostisch und sind hellgrau schattiert; Arten mit einem *phi*-Wert größer als 0,50 gelten als hochdiagnostisch und sind dunkelgrau schattiert. Arten, die in einem Cluster hochdiagnostisch oder diagnostisch sind, werden als diagnostisch für Verbände akzeptiert; Arten, die in mehr als einem Cluster hochdiagnostisch oder diagnostisch sind, werden als diagnostisch für hochrangige Syntaxa akzeptiert. Arten mit einer Stetigkeit von 15 % oder weniger in einzelnen Spalten werden in der Tabelle nicht angezeigt, es sei denn, sie sind diagnostisch.

ID clusters	1	2	3	4	5	6
Number of relevés	35	11	73	243	92	28
All. <i>Anabasio cretaceae</i>-<i>Agropyron desertori</i>						
<i>Astragalus kustanaicus</i>	63	.	.	.	.	.
<i>Bassia prostrata</i>	89	9	19	5	2	2
<i>Sterigmotemum caspicum</i>	69	9	7	.	.	.
<i>Galatella tatarica</i>	57	.	4	.	.	.
<i>Agropyron cristatum</i> aggr.	94	.	52	1	1	6
<i>Krascheninnikovia ceratoides</i>	63	.	7	5	3	1
<i>Tulipa scythica</i>	49	.	5	.	.	.
<i>Lappula microcarpa</i>	63	.	27	.	.	.
<i>Allium tulipifolium</i>	43	.	7	.	.	.
<i>Tulipa biflora</i>	37	.	1	.	.	.
<i>Tulipa sylvestris</i>	37	.	1	.	.	.
<i>Tragopogon ruber</i>	40	.	5	.	.	.
<i>Poa bulbosa</i>	40	.	4	1	.	5
<i>Taraxacum</i> sect. <i>Macrocornuta</i>	31	.	1	.	.	.
<i>Isatis gymnocarpa</i>	29	.	.	.	.	.
<i>Asparagus inderiensis</i>	34	.	7	.	.	.
<i>Meniocus linifolius</i>	37	.	1	.	.	1
<i>Litwinowia tenuissima</i>	23	.	.	.	.	.
<i>Stipa sareptana</i>	46	18	12	.	.	.
<i>Caragana balchaschensis</i>	23	.	1	.	.	.
<i>Ferula caspica</i>	23	.	3	.	.	.
<i>Palimbia turgaica</i>	23	.	3	.	.	.
<i>Gagea bulbifera</i>	17	.	.	.	.	.
<i>Pseudosedum lievenii</i>	17	.	.	.	.	.
<i>Rochelia disperma</i> subsp. <i>retorta</i>	17	.	.	.	.	.
<i>Limonium meyeri</i>	17	.	.	.	.	.
<i>Allium lineare</i>	17	.	.	.	.	.
<i>Rindera tetraspis</i>	31	18	.	.	.	.
<i>Artemisia semiarida</i>	31	18	3	.	.	.
<i>Eriosynaphe longifolia</i>	14	.	.	.	.	.
<i>Astragalus temirensis</i>	14	.	.	.	.	.
<i>Tulipa suaveolens</i>	14	.	.	.	.	.
<i>Anabasis salsa</i>	23	9	.	.	.	.
<i>Filago arvensis</i>	14	.	.	.	.	.
<i>Klasea erucifolia</i>	14	.	.	.	.	.

ID clusters	1	2	3	4	5	6
Number of relevés	35	11	73	243	92	28
<i>Silene otites</i> aggr.	14	.	.	.	.	1
<i>Linaria incompleta</i>	20	.	7	.	.	.
<i>Artemisia lessingiana</i>	29	.	21	.	.	.
<i>Androsace maxima</i>	17	.	5	.	.	.
<i>Allium inderiense</i>	11	.	.	.	.	.
<i>Silene viscosa</i>	11	.	.	.	.	.
<i>Takhtajaniantha pusilla</i>	11	.	.	.	.	.
<i>Ixiolirion tataricum</i>	11	.	.	.	.	.
<i>Ornithogalum fischerianum</i>	11	.	.	.	.	1
All. <i>Sileno fruticosae</i>-<i>Nanophyton erinacei</i>						
<i>Matthiola tatarica</i>	.	100	.	.	.	.
<i>Gypsophila diffusa</i>	.	100	.	.	.	.
<i>Onosma staminea</i>	.	91	.	.	.	.
<i>Nanophyton erinaceum</i>	11	91	18	.	.	.
<i>Atraphaxis spinosa</i>	.	64	.	.	.	.
<i>Artemisia terrae-albae</i>	3	64	.	.	.	.
<i>Atraphaxis replicata</i>	3	64	.	.	.	.
<i>Galium humifusum</i>	.	64	.	1	.	3
<i>Silene antri-jovis</i>	.	55	4	.	.	.
<i>Lepidium meyeri</i>	.	73	25	4	.	.
<i>Lomelosia isetensis</i>	6	73	25	.	.	.
<i>Anabasis cretacea</i>	46	100	6	.	.	.
<i>Astragalus medius</i>	3	36	1	.	.	.
<i>Astragalus stenoceras</i>	.	27	.	.	.	.
<i>Rhammatophyllum pachyrhizum</i>	.	27	1	.	.	.
<i>Limonium suffruticosum</i>	3	27	.	.	.	.
<i>Ephedra distachya</i>	34	73	47	.	9	3
<i>Convolvulus fruticosus</i>	.	18	.	.	.	.
All. <i>Anthemido trotzkiana</i>-<i>Artemision salsoloides</i>						
<i>Archanthemis trotzkiana</i>	6	.	90	.	.	.
<i>Zygophyllum pinnatum</i>	.	9	67	.	.	.
<i>Atraphaxis decipiens</i>	.	.	48	.	.	.
<i>Matthiola fragrans</i>	3	.	82	45	10	6
<i>Astragalus tenuifolius</i>	23	.	56	.	.	.
<i>Hedysarum tscherkassovae</i>	3	.	36	.	.	.
<i>Jurinea kirghisorum</i>	.	.	25	.	.	.
<i>Gypsophila rupestris</i>	.	.	21	.	.	.
<i>Artemisia salsoloides</i>	9	.	74	33	53	15
<i>Hedysarum razoumovianum</i>	3	.	18	.	.	.
<i>Gypsophila altissima</i>	.	.	12	.	.	.
<i>Galium octonarium</i>	9	.	27	9	1	5
<i>Atraphaxis frutescens</i>	.	.	14	2	.	.
All. <i>Sileno supinae</i>-<i>Artemision hololeuca</i>						
<i>Hyssopus officinalis</i>	.	.	.	81	8	10
<i>Scrophularia cretacea</i>	.	.	.	52	13	6
<i>Artemisia hololeuca</i>	.	.	.	48	4	12
<i>Festuca cretacea</i>	.	.	.	18	1	1
<i>Asperula tephrocarpa</i>	.	.	.	62	55	48
<i>Plantago maritima</i> subsp. <i>ciliata</i>	.	.	.	16	.	6
All. <i>Euphorbio cretophilae</i>-<i>Thymion cretacei</i>						
<i>Euphorbia petrophila</i>	.	.	.	7	84	5
<i>Jurinea stoechadifolia</i>	.	.	.	1	73	7
<i>Helianthemum canum</i> aggr.	.	.	.	2	28	2
<i>Hedysarum grandiflorum</i>	.	.	1	2	32	10

ID clusters	1	2	3	4	5	6
Number of relevés	35	11	73	243	92	28
<i>Reseda lutea</i>	.	.	1	23	55	38
<i>Genista scythica</i>	.	.	.	.	20	1
<i>Linum tenuifolium</i>	.	.	.	5	25	4
<i>Onosma simplicissima</i>	3	.	11	14	49	38
<i>Leontodon crispus</i> aggr.	.	.	.	.	16	5
<i>Rhaponticoides talievii</i>	.	.	.	.	11	.
All. <i>Centaureo carbonatae</i>-<i>Koelerion talievii</i>						
<i>Carex humilis</i>	.	.	.	2	3	44
<i>Stipa pennata</i>	.	.	.	2	1	33
<i>Festuca valesiaca</i> aggr.	9	.	7	9	5	51
<i>Viola ambigua</i>	.	.	.	1	5	33
<i>Polygala sibirica</i>	.	.	.	6	1	33
<i>Bromopsis riparia</i>	.	.	.	2	8	35
<i>Stipa capillata</i>	3	.	3	4	15	44
<i>Bupleurum falcatum</i>	.	.	.	16	18	45
<i>Securigera varia</i>	.	.	.	4	9	31
<i>Koeleria talievii</i>	.	.	.	7	10	34
<i>Euphorbia seguieriana</i>	34	9	10	25	8	64
<i>Campanula sibirica</i>	.	.	.	5	35	44
<i>Stachys recta</i>	.	.	.	3	5	26
<i>Salvia nutans</i>	.	.	.	1	29	39
<i>Achillea millefolium</i> aggr.	.	.	.	.	.	16
<i>Astragalus austriacus</i>	.	.	1	1	1	20
<i>Medicago falcata</i>	3	.	1	5	7	29
<i>Scabiosa ochroleuca</i>	.	.	.	7	10	29
<i>Vincetoxicum hirundinaria</i>	.	.	.	2	21	31
<i>Androsace villosa</i>	.	.	.	5	.	19
<i>Polygala cretacea</i>	.	.	1	26	9	36
<i>Ajuga chamaepitys</i>	.	.	.	.	.	11
<i>Jurinea mollis</i> aggr.	.	.	.	5	5	20
<i>Euphorbia nicaeensis</i>	.	.	.	9	3	21
<i>Helianthemum nummularium</i>	.	.	.	.	2	13
Ord. <i>Anabasietaalia cretaceae</i>						
<i>Psathyrostachys juncea</i>	49	.	38	1	.	.
<i>Seseli glabratum</i>	14	82	89	.	.	.
Ord. <i>Thymo cretacei</i>-<i>Hyssopetalia cretacei</i>						
<i>Pimpinella tragioides</i>	.	.	4	86	83	58
<i>Cephalaria uralensis</i>	.	.	11	60	70	29
<i>Teucrium polium</i>	.	.	.	20	75	68
<i>Thymus calcareus</i>	.	.	.	70	87	83
<i>Gypsophila oligosperma</i>	.	.	.	57	71	66
Other taxa occurred in the communities						
<i>Thalictrum minus</i>	.	.	.	.	23	26
<i>Astragalus albicaulis</i>	.	.	.	23	13	32
<i>Poa compressa</i>	.	.	.	11	4	19
<i>Salvia verticillata</i>	.	.	.	3	11	18
<i>Erysimum diffusum</i>	6	.	3	3	15	23
<i>Helichrysum arenarium</i>	.	.	.	13	20	25
<i>Linum flavum</i> aggr.	.	.	.	37	47	40
<i>Linum hirsutum</i>	.	.	.	7	23	22
<i>Silene supina</i>	.	.	.	28	22	26
<i>Psephellus marschallianus</i> aggr.	34	.	36	5	34	34
<i>Thesium ramosum</i>	.	.	3	13	12	16
<i>Stipa lessingiana</i>	14	.	21	4	13	18

ID clusters	1	2	3	4	5	6
Number of relevés	35	11	73	243	92	28
<i>Artemisia lerchiana</i>	37	18	33	2	.	1
<i>Brassica elongata</i>	23	.	23	14	38	17
<i>Odontarrhena tortuosa</i> aggr.	6	.	33	2	38	9
<i>Genista tinctoria</i> aggr.	.	.	.	19	21	14
<i>Odontites luteus</i>	.	.	.	13	16	6
<i>Echinops ritro</i>	23	45	41	5	4	14
<i>Crambe tataria</i> aggr.	11	.	22	3	.	2
<i>Camphorosma monspeliaca</i>	11	.	15	.	.	.

Cluster 1

35 relevés (Table 1, Fig. 3, 4)

Diagnostic species: *Agropyron cristatum* aggr., *Allium inderiense*, *A. lineare*, *A. tulipifolium*, *Anabasis salsa*, *Androsace maxima*, *Artemisia lessingiana*, *A. semiarida*, *Asparagus inderiensis*, *Astragalus kustanaicus*, *A. temirensis*, *Bassia prostrata*, *Caragana balchaschensis*, *Eriosynaphe longifolia*, *Ferula caspica*, *Filago arvensis*, *Gagea bulbifera*, *Galatella tatarica*, *Isatis gymnocarpa*, *Ixiolirion tataricum*, *Klasea erucifolia*, *Krascheninnikovia ceratoides*, *Limonium meyeri*, *Linaria incompleta*, *Litwinowia tenuissima*, *Meniocus linifolius*, *Ornithogalum fischerianum*, *Palimbia turgaica*, *Poa bulbosa*, *Psathyrostachys juncea*, *Pseudosedum lievenii*, *Rindera tetraspis*, *Rochelia disperma* subsp. *retorta*, *Silene otites* aggr., *S. viscosa*, *Sterigmostemum caspicum*, *Stipa sareptana*, *Takhtajaniantha pusilla*, *Taraxacum* sect. *Macrocornuta*, *Tragopogon ruber*, *Tulipa biflora*, *T. scythica*, *T. suaveolens*, *T. sylvestris*.

Ecology and distribution: These communities occur at the feet of chalk hills, on alluvial fans of chalk bedrocks and chalk plateau peaks facing south, and south-western slopes with an inclination of 30–75° of the Sub-Ural Upland (Kazakhstan). They are apparently the latest stage of the chalk overgrowth and are transitional between *Festuco-Brometea* and *Anabasi-etalia cretaceae* order *nom. inv.* (Golovanov et al. 2021).

Cluster 2

11 relevés (Table 1, Fig. 3, 4)

Diagnostic species: *Anabasis cretacea*, *Artemisia terrae-albae*, *Astragalus medius*, *A. stenoceras*, *Atraphaxis replicata*, *A. spinosa*, *Convolvulus fruticosus*, *Ephedra distachya*, *Galium humifusum*, *Gypsophila diffusa*, *Lepidium meyeri*, *Limonium suffruticosum*, *Lomelosia isetensis*, *Matthiola tatarica*, *Nanophyton erinaceum*, *Onosma staminea*, *Rhammatophyllum pachyrhizum*, *Seseli glabratum*, *Silene antri-jovis*.

Ecology and distribution: These communities occur on chalk outcrops on slopes facing south to north and northwest in northern deserts and desert steppes in the arid conditions of the Sub-Ural Upland (Kazakhstan and partly Russian Federation). They occupy scree slopes with an inclination of 30–75° (Golovanov et al. 2021).

Cluster 3

73 relevés (Table 1, Fig. 3,4)

Diagnostic species: *Archanthemis trotzkiana*, *Artemisia salsoloides*, *Astragalus tenuifolius*, *Atraphaxis decipiens*, *A. frutescens*, *Galium octonarium*, *Gypsophila altissima*, *G. rupestris*, *Hedysarum razoumovianum*, *H. tscherkassovae*, *Jurinea kirghisorum*, *Matthiola fragrans*, *Psathyrostachys juncea*, *Seseli glabratum*, *Zygophyllum pinnatum*.

Ecology and distribution: These communities occur on chalk uplands with gravel substrates or eroded and loose chalk outcrops on slopes facing mainly to the north of the Sub-Ural and partly Obshchy Syrt Uplands (Kazakhstan). They occupy scree slopes with an inclination of 15–60° (Golovanov et al. 2021).

Cluster 4

243 relevés (Table 1, Fig. 3, 4)

Diagnostic species: *Artemisia hololeuca*, *Asperula tephrocarpa*, *Cephalaria uralensis*, *Festuca cretacea*, *Hyssopus officinalis*, *Pimpinella tragioides*, *Plantago maritima* subsp. *ciliata*, *Scrophularia cretacea*.

Ecology and distribution: These communities occur on chalk outcrops at elevations of 70–140 m a.s.l. on scree slopes (15–65°) facing north to northwest on the right banks of river valleys. They occur on loose substrates caused by denudation and cover surface erosion. Relevés belonging to this cluster were recorded in the Central Russian Upland, Donetsk Ridge (Ukraine and Russian Federation). The layer of bryophytes and lichens is consisted of *Enchylium tenax*, *Geheebia fallax*, *Syntrichia ruralis*, *Weissia levieri*.

Cluster 5

92 relevés (Table 1, Fig. 3, 4)

Diagnostic species: *Cephalaria uralensis*, *Euphorbia petrophila*, *Genista scythica*, *Gypsophila oligosperma*, *Hedysarum grandiflorum*, *Helianthemum canum* aggr., *Jurinea stoechadifolia*, *Leontodon crispus* aggr., *Linum tenuifolium*, *Onosma simplicissima*, *Pimpinella tragioides*, *Reseda lutea*, *Rhaponticoides talievii*, *Teucrium polium*, *Thymus calcareus*.

Ecology and distribution: These communities occur on the lowest line of gentle chalk slopes (5–40°) facing south and southwest of river valleys. They indicate the final stage of overgrowing and transformation into pure grasslands. These communities occupy dense diluvium with carbonate and sulphate soil salinization and occur in the Central Russian Upland, Donetsk Ridge, and Eastern Don Ridge (Ukraine, Russian Federation).

Cluster 6

280 relevés (Table 1, Fig. 3, 4)

Diagnostic species: *Achillea millefolium* aggr., *Ajuga chamaepitys*, *Androsace villosa*, *Astragalus austriacus*, *Bromopsis riparia*, *Bupleurum falcatum*, *Campanula sibirica*, *Carex humilis*, *Euphorbia nicaeensis*, *E. seguieriana*, *Festuca valesiaca* aggr., *Gypsophila oligosperma*, *Helianthemum nummularium*, *Jurinea mollis* aggr., *Koeleria talievii*, *Medicago falcata*, *Polygala cretacea*, *P. sibirica*, *Salvia nutans*, *Scabiosa ochroleuca*, *Securigera varia*, *Stachys recta*, *Stipa capillata*, *S. pennata*, *Teucrium polium*, *Thymus calcareus*, *Vincetoxicum hirsutum*, *Viola ambigua*.

Ecology and distribution: These communities occur on depths of chalk outcrops at elevations of 75–145 m a.s.l. on slopes facing north and northeast on which rendzic leptosols have accumulated. They occur in the Central Russian Upland, Donetsk Ridge (Ukraine and Russian Federation). The layer of bryophytes and lichens is consisted of *Barbula unguiculata*, *Ceratodon purpureus*, *Cladonia rei*, *Enchylium tenax*, *Homalothecium lutescens*, *Syntrichia ruralis*, *Trichostomum crispulum*, *Weissia longifolia*.

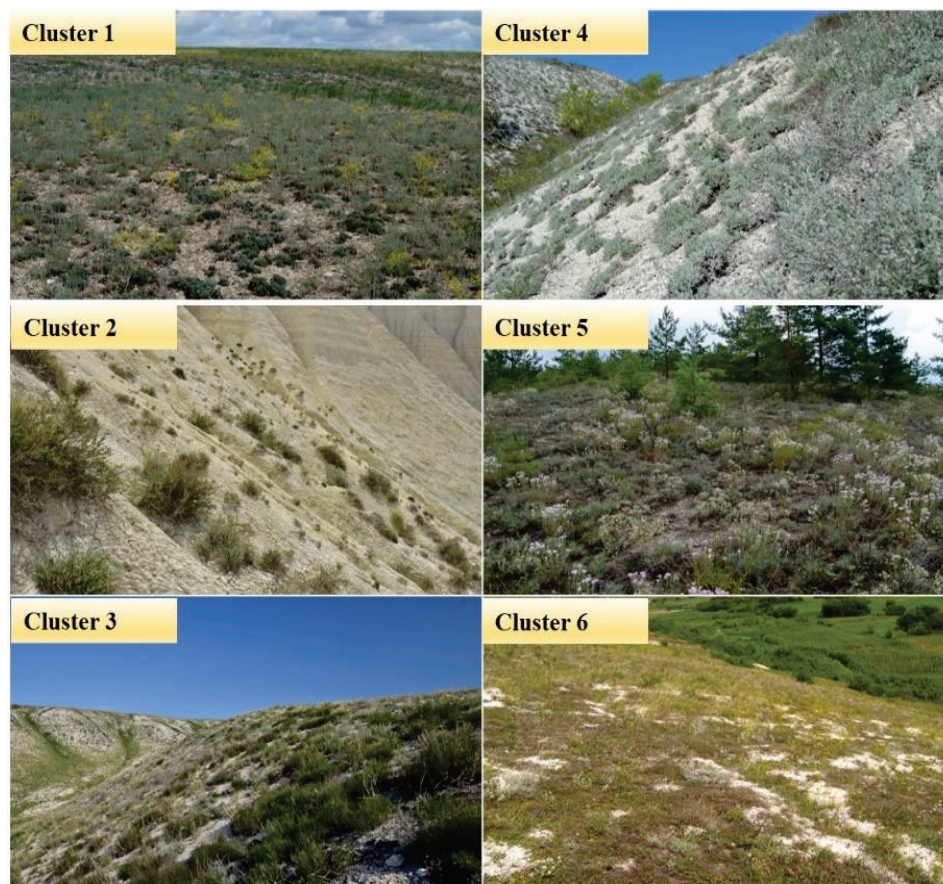


Fig. 3. Chalk rocky grasslands within the Eastern European Plain. Cluster 1 – *Anabasio cretaceae-Agropyrion desertori* (Troitsk Chalk Hills, adjacent territories of Kazakhstan, 2019); Cluster 2 – *Sileno fruticosae-Nanophytion erinacei* (Aktolagai Ridge, Kazakhstan, 2019); Cluster 3 – *Anthemido troitzkianae-Artemision salsoloides* (Troitsk Chalk Hills, adjacent territories of Kazakhstan, 2019); Cluster 4 – *Sileno supinae-Artemision hololeucae* (Krasna valley, Svatove, Ukraine, 2014); Cluster 5 – *Euphorbio cretophilae-Thymion cretacei* (“Kreidova Flora” Nature Reserve, Ukraine, 2019); Cluster 6 – *Centaureo carbonatae-Koelerion talievii* (Krasna valley, Honcharivka, Ukraine, 2013) (Photos: cited from Golovanov et al. 2021 (1–3), O. Chusova (4–6)).

Abb. 3. Kalkfelsrasen in der osteuropäischen Tiefebene. Cluster 1 – *Anabasio cretaceae-Agropyrion desertori* (Troizker Kreidehügel, angrenzende Gebiete Kasachstans, 2019); Cluster 2 – *Sileno fruticosae-Nanophytion erinacei* (Aktolagai-Rücken, Kasachstan, 2019); Cluster 3 – *Anthemido troitzkianae-Artemision salsoloides* (Troizker Kreidehügel, angrenzende Gebiete Kasachstans, 2019); Cluster 4 – *Sileno supinae-Artemision hololeucae* (Krasna-Tal, Svatove, Ukraine, 2014); Cluster 5 – *Euphorbio cretophilae-Thymion cretacei* (Naturschutzgebiet „Kreidova Flora“, Ukraine, 2019); Cluster 6 – *Centaureo carbonatae-Koelerion talievii* (Krasna-Tal, Honcharivka, Ukraine, 2013) Fotos: zitiert nach Golovanov et al. 2021 (1–3), O. Chusova (4–6)).

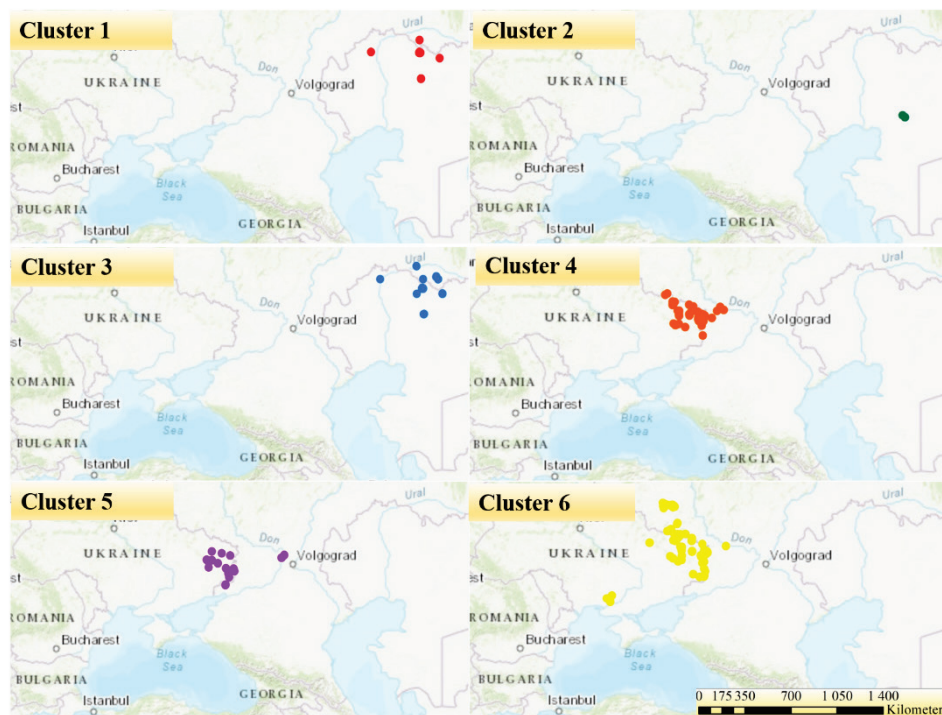


Fig. 4. Maps of the chalk rocky grasslands distribution (alliance level). Abbreviations are the same as in Figure 3.

Abb. 4. Verbreitungskarten der Kalkfelsrasen auf der Verbandsebene. Die Abkürzungen entsprechen denen in Abbildung 3.

Proposed syntaxonomic scheme

??? Class: *Helianthemo-Thymetea* Romashchenko et al. 1996

Order: *Anabasieta lia cretaceae* Golovanov et al. ex Vasheniak et al. 2024

Alliance: *Anabasio cretaceae-Agropyron desertori* Golovanov et al. 2021

Alliance: *Sileno fruticosae-Nanophytion erinacei* Golovanov et al. 2021

Alliance: *Anthemido trotziana-Artemision salsoloides* Golovanov et al. 2021

Order: *Thymo cretacei-Hyssopetalia cretaceae* Didukh ex Romashchenko et al. 1996

Alliance: *Sileno supinae-Artemision hololeuca* Didukh 1989 (*Artemisia hololeuca-Hyssopion cretacei* Romashchenko et al. 1996 nom. superfl.)

Alliance: *Euphorbio cretophilae-Thymion cretacei* Didukh ex Vasheniak et al. 2024

Transitional communities between *Helianthemo-Thymetea* and *Festuco-Brometea*

Alliance: *Centaureo carbonatae-Koelerion talievii* Romashchenko et al. 1996

4.2 Environmental differences within chalk rocky grasslands

Detrended correspondence analysis (DCA) shows the differentiation of chalk rocky grasslands (*Anabasi-etalia cretaceae*, *Thymo cretacei-Hyssopetalia cretaceae* orders) and other types of calcareous rocky grasslands (*Stipo pulcherrimae-Festucetalia pallentis* order) across the DCA2 axis where the vector of reaction lays within the DCA2 axis plane (Fig. 5). This differentiation is caused by variable calcareous bedrocks with high calcium ion content of chalks and lower in marls, dolomites and limestones, which affects the soil reaction.

Generally, a clear ecological distinction between chalk and other calcareous rocky grasslands can be observed; however, differentiation is also noticeable within the *Anabasi-etalia cretaceae* and *Thymo cretacei-Hyssopetalia cretaceae* group along the gradient of nitrogen, temperature and light. Therefore, we will focus more closely on the chalk rocky grasslands at the alliance level, using a broader range of ecological indicators based on Didukh's scales.

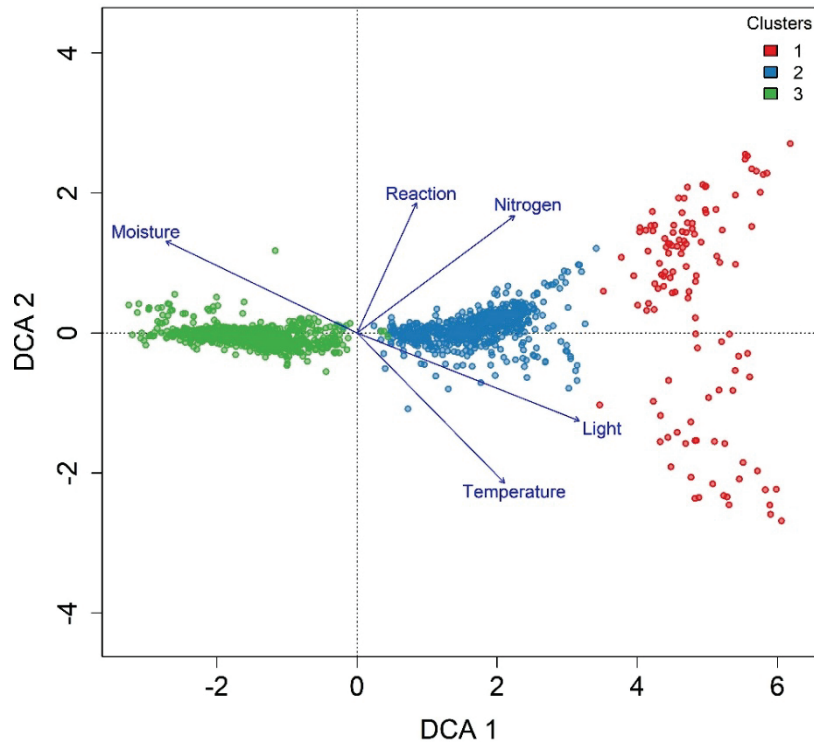


Fig. 5. DCA ordination of *Anabasi-etalia cretaceae* (1), *Thymo cretacei-Hyssopetalia cretaceae* (2), *Stipo pulcherrimae-Festucetalia pallentis* (3) based on EIVE 1.0 scales with passively projected mean indicator values.

Abb. 5. DCA-Ordination der *Anabasi-etalia cretaceae* (1), *Thymo cretacei-Hyssopetalia cretaceae* (2), *Stipo pulcherrimae-Festucetalia pallentis* (3) basierend auf EIVE 1.0-Skalen mit passiv projizierten mittleren Indikatorwerten.

According to Figure 6, chalk rocky grasslands differentiate across the DCA2 axis. The vectors of cryoregime, aeration, variation of damping and carbonate content indicators lie in the DCA1 axis plane. On the other hand, the vectors of nitrogen content and thermoregime lie in the DCA2 axis plane, where two groups (1–3 and 4–6) of chalk rocky grasslands are differentiated. Additionally, communities differ within the salt regime, continentality and light vectors, whereas communities of *Sileno fruticosae-Nanophytion erinacei* occupy an extreme position of ecological values. This differentiation is caused by the increasing continentality, surface illumination, considerable evaporation and further salinisation of the communities in Kazakhstan compared with Ukraine and Russian Federation. All communities vary within the reaction indicator vector, where communities of *Sileno fruticosae-Nanophytion erinacei* and *Anthemido trotzkianae-Artemision salsoloides* occupy the extreme position of the reaction indicator.

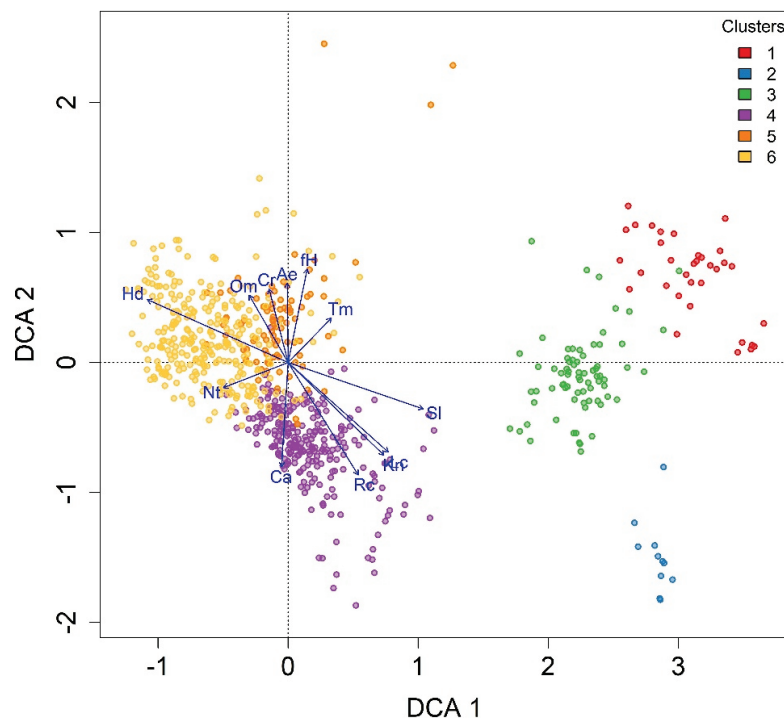


Fig. 6. DCA ordination of chalk rocky grasslands based on Didukh' scales with passively projected mean indicator values. **Abbreviations:** 1 – *Anabasio cretaceae-Agropyron desertori*, 2 – *Sileno fruticosae-Nanophytion erinacei*, 3 – *Anthemido trotzkianae-Artemision salsoloides*, 4 – *Sileno supinae-Artemision hololeuca*, 5 – *Euphorbio cretophilae-Thymion cretacei*, 6 – *Centaureo carbonatae-Koelerion talievii*. **Acronyms:** Hd – soil humidity, fH – variability of damping, Rc – soil acidity, Sl – total salt regime, Ca – carbonate content, Nt – nitrogen content, Ae – soil aeration, Tm – thermoregime, Om – humidity of microclimate, Kn – continentality, Cr – cryoregime, Lc – light in the community.

Abb. 6. DCA-Ordination von Kreidefelsrasen basierend auf Didukh-Skalen mit passiv projizierten mittleren Indikatorwerten. **Abkürzungen** der Verbände s.o. **Akronyme:** Hd – Bodenfeuchte, fH – Variabilität der Feuchtigkeit, Rc – Säuregehalt des Bodens, Sl – Gesamtsalzregime, Ca – Karbonatgehalt, Nt – Stickstoffgehalt, Ae – Bodenbelüftung, Tm – Thermoregime, Om – Feuchtigkeit des Mikroklimas, Kn – Kontinentalität, Cr – Kryoregime, Lc – Licht in der Gesellschaft.

To gain a better understanding of the structure and ecological characteristics of chalk rocky grasslands, which distinguish them from other types of grasslands, we carried out further analyses of life forms and ecological strategies to compare six syntaxa of chalk rocky grasslands with seven syntaxa of other types of calcareous rocky grasslands at the alliance level (see Supplement E4).

Life forms determine the structure, character of development, dynamics and resistance of coenoses to the influence of external factors; they, therefore, have significant diagnostic value. According to Figure 7, there is an apparent gap between chalk rocky grasslands and rocky grasslands of the *Stipo pulcherrimae-Festucetalia pallentis* order (Supplement E4). Communities belonging to the *Stipo pulcherrimae-Festucetalia pallentis* order have a significantly higher proportion of hemicryptophytes, the highest in the case of the *Seslerion rigidae* alliance (Fig. 7). In contrast, communities of the *Helianthemo-Thymetea* class have a much lower representation of hemicryptophytes but a much higher proportion of chamaephytes (Fig. 7), which is exceptionally high in the case of the alliances *Anthemido trotzkianae-Artemision salsoloides* and *Sileno fruticosae-Nanophytion erinacei*. An equal proportion of hemicryptophytes and chamaephytes is characteristic of the *Anabasio cretaceae-Agropyron desertori* and *Centaureo carbonatae-Koelerion talievii* alliances.

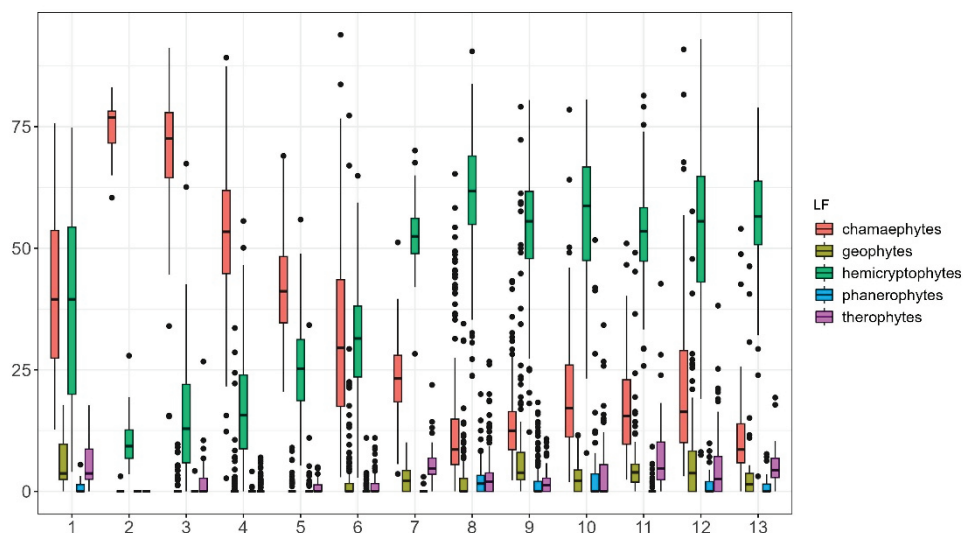


Fig. 7. Life forms of the distinguished thirteen clusters that represent chalk rocky grasslands compared with other types of calcareous grasslands (alliance level).

Abbreviations: 1 – *Anabasio cretaceae-Agropyron desertori*; 2 – *Sileno fruticosae-Nanophytion erinacei*; 3 – *Anthemido trotzkianae-Artemision salsoloides*; 4 – *Sileno supinae-Artemision hololeuca*; 5 – *Euphorbio cretophilae-Thymion cretacei*; 6 – *Centaureo carbonatae-Koelerion talievii*; 7 – *Seseli leucospermum-Fumana procumbens* grasslands; 8 – *Seslerion rigidae*; 9 – *Sesleria caerulea-Leontodon incanus* grasslands; 10 – *Asplenio septentrionalis-Festucion pallentis*; 11 – *Bromo pannonicus-Festucion pallentis*; 12 – *Galio campanulati-Poion versicoloris*; 13 – *Linum catharticum-Galium cracoviense* grasslands.

Abb. 7. Lebensformen der dreizehn unterschiedenen Cluster, die die Kalkfelsrasen im Vergleich mit anderen Typen von Kalkmagerrasen darstellen (Verbandsebene). Abkürzungen der Syntaxa s. englische Abbildungsunterschrift.

According to the ecological strategies of Grime, chalk rocky grasslands are located in the fields (S, SC) close to S ($> 50\%$), $C < 50\%$ and $R < 75\%$ with the dominance of stress-tolerant and stress-tolerant/competitor species. On the other hand, the calcareous rocky grasslands of *Stipo pulcherrimae-Festucetalia pallentis* are located within the CS field (Fig. 8).

SPE habitats occur at reach conditions, absorb and transform resources and energy and develop within the successional range. When the “centres of mass” approach the C peak, the mentioned parameters increase (Didukh 2023). FLE habitats are characterized by high lability, the stability of which is due to rapid reproduction after the destruction and high species flexibility caused by fluctuations characterised by resource and energy accumulation and rapid transmission (Didukh 2023). According to Figur 8, “centres of mass” do not occur in the R field, and fluctuations are not characteristic of FLE habitats.

PSE habitats occur within extreme conditions caused by maximum and minimum indices of factors that limit resource consumption. These communities are stable in relation to environmental impact, highly resistant, with limited successional changes, and exist indefinitely with weakly expressed development stages. PSE habitats develop slowly and express themselves in speciation processes due to changes in the morphological and anatomical features of organs as a specialization of adaptation mechanisms to external conditions of existence (Didukh 2023). When the “centres of mass” of chalk rocky grasslands approach the S peak, the mentioned parameters are characteristic, and chalk rocky grasslands differ from pure steppes and reflect high conservatism. Notably, the *Anabasio cretaceae-Agropyron desertori*, *Sileno fruticulosae-Nanophytion erinacei*, and *Anthemido trotzkianae-Artemision salsoloides* communities are the closest to the PSE field and could be characterized as the persistent stable ecosystems (Fig. 8). Thus, neither successions nor fluctuating processes are distinct, which is essential to consider in developing management measures for their conservation.

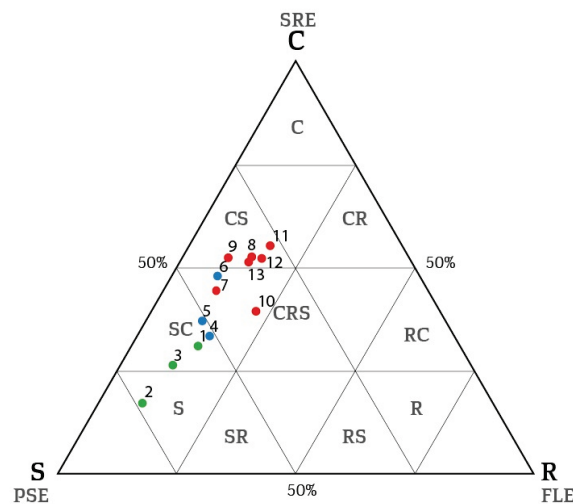


Fig. 8. The ecological strategy of the distinguished thirteen clusters that represent chalk rocky grasslands compared with other types of calcareous grasslands (alliance level). Abbreviations are the same as in the Figure 6.

Abb. 8. Die ökologische Strategie der dreizehn unterschiedenen Cluster, die Kalkfelsrasen im Vergleich zu anderen Arten von Kalkmagerrasen repräsentieren (Verbandsebene). Die Abkürzungen sind dieselben wie in Abbildung 6.

4.3 Syntaxonomical revision

Continental arid steppe zone that unifies meso-xerophytic grasslands on deep calcareous soils of Western and Central Europe that are classified within the *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947. When conditions become more arid, European steppes give way to the semi-desert and desert steppe vegetation within the continental arid semidesert zone that syntaxonomically classified as the *Artemisietea lerchianae* Golub 1994 (Mucina et al. 2016, 2024). However, zonal vegetation of *Festuco-Brometea* and *Artemisietea lerchianae* occur on deep soils of different genesis where the correlation of edaphic and climate environmental parameters is significant (Didukh 2023). What about the cretaceous vegetation that occurs on shallow soils on chalk outcrops if they are variations of zonal vegetation?

Chalk rocky vegetation is floristically and ecologically different from the zonal steppe vegetation of *Festuco-Brometea* and *Artemisietea lerchianae* and was considered within two classes: *Helianthemo-Thymetea* and *Anabasietaea cretaceae nom. inv.* (Romashchenko et al. 1996, Didukh et al. 2018, Golovanov et al. 2021).

The *Thymo cretacei-Hyssopetalia cretacei* order, designated by Didukh (1989) as *Thymo-Hyssopetalia* in the original diagnosis, has the nomenclature type of the *Euphorbio cretophilae-Thymion* alliance. On the other hand, the *Euhorbio cretaceae-Thymion cretaceae* alliance was probably mistakenly provided in the original diagnosis (Art. 41a), rather than the *Euphorbio cretophilae-Thymion cretaceae* alliance, and it has the nomenclature type of the *Euphorbio cretaceae-Jurinetum brachycephalae* association (Didukh 1989). The name of the *Euphorbio cretophilae-Jurinetum brachycephalae* association is invalid (Art. 3f) since there is “*Euphorbia cretacea*” in the original diagnosis (Table 2, p. 19 in Didukh 1989); however, these taxa does not exist since it is not listed in Euro+Med PlantBase (<https://www.emplantbase.org/>). According to Art. 3f (Theurillat et al. 2021), the *Euphorbio cretophilae-Thymion* alliance and *Thymo-Hyssopetalia* order are invalidly published due to invalidly published *Euphorbio cretophilae-Jurinetum brachycephalae* association.

Romashchenko et al. (1996) later designated the illegitimate *Artemisio hololeucae-Hyssopion cretacei* Romashchenko et al. 1996 as a type of the *Thymo cretacei-Hyssopetalia cretacei* order and *de facto* validated the *Thymo-Hyssopetalia* order. The *Artemisio hololeucae-Hyssopion cretaceae* alliance is validly published, and the nomenclature type of the alliance is the *Artemisio hololeucae-Polygaletum cretaceae* association. Romashchenko et al. (1996) designated *Artemisio hololeucae-Polygaletum cretaceae* Didukh 1989 as the nomenclatural type of this alliance. However, Romashchenko et al. (1996) further indicated that this alliance is identical to *Sileno supinae-Artemision hololeucae* Didukh 1989. This means that *Artemisio hololeucae-Hyssopion cretaceae* Romashchenko et al. 1996 is “superfluous” (Art. 29c), hence the illegitimate name of *Sileno supinae-Artemision hololeucae* Didukh 1989. The *Sileno supinae-Artemision hololeucae* alliance is validly published by Didukh (1989) and designated the valid *Sileno supinae-Matthioletum fragrantis* association. The nomenclature type of the *Thymo cretacei-Hyssopetalia cretacei* order is, therefore, the *Sileno supinae-Artemision hololeucae* alliance.

Regarding the class *Anabasietaea cretaceae* and order *Anabasietalia cretaceae*, the nomenclature types of high-rank syntaxa have been provided mistakenly and invalidly published (Art.8) (Theurillat et al. 2021). The nomenclature type of the order *Anabasietalia cretaceae* and class *Anabasietaea cretaceae* is the *Anthemido trotzkianae-Artemisietum salsoloidis* association, despite the selected names of the alliance and order, respectively (Golovanov et al. 2021).

Regarding the *Helianthemo-Thymetea*, the nomenclature type of the class is the *Thymo cretacei-Hyssopetalia cretacei* order (Art. 8). Romashchenko et al. (1996) have validated the class in their paper, although they have not explicitly cited correct name “*Thymo cretacei-Hyssopetalia cretacei* Didukh ex Romashchenko et al. 1996” according to the Code (Theurillat et al. 2021). Mucina et al. (2016) do not consider this class in its own right and assign chalk rocky grasslands within the *Festuco-Brometea* class. However, chalk rocky grasslands sharply differentiate from the closer type of vegetation that occurs on calcareous outcrops (*Stipo pulcherrimae-Festucetalia pallentis*) (Fig. 2) and have their own diagnostic species (e.g. *Artemisia salsoloides*, *Cephalaria uralensis*, *Pimpinella tragium*). On the other hand, there are many species (e.g. *Asperula cynanchica*, *Campanula sibirica*, *Festuca valesiaca* aggr.) with high constancy that are considered diagnostic for *Festuco-Brometea*; therefore, we have preliminarily assigned chalk rocky grasslands within *Helianthemo-Thymetea* class” (Kuzemko & Khodosovtsev 2022) with question marks “???”.

4.4 Validation of the chalk rocky grasslands syntaxa

We propose to designate the nomenclature type of the *Euphorbio cretophilae-Jurinetum brachycephalae* association from Romashchenko et al. (1996) and validate the name of the association (Art. 2b):

Association *Euphorbio cretophilae-Jurinetum brachycephalae* Didukh ex Vasheniak et al. 2024

Neotypus hoc loco: Romashchenko et al. (1996), page 57, table 3, relevé 24.

Diagnostic species: according to Romashchenko et al. (1996): *Centaurea lavrenkoana*, *Cytisus ruthenicus*, *Genista tinctoria*, *Helichrysum arenarium*, *Linum austriacum*, *Minuartia setacea*, *Odontarrhena tortuosa*.

The name of the *Euphorbio cretophilae-Jurinetum brachycephalae* association is assigned by the authors (Romashchenko et al. 1996) as the nomenclature type of the alliance *Euphorbio cretophilae-Thymion cretacei* alliance. We propose validating the alliance name according to the association's validation (Art. 2b, 8).

Alliance *Euphorbio cretophilae-Thymion cretacei* Didukh ex Vasheniak et al. 2024

Neotypus hoc loco: *Euphorbio cretophilae-Jurinetum brachycephalae* Didukh ex Vasheniak et al. 2024.

Diagnostic species: according to Romashchenko et al. (1996): *Artemisia salsoloides*, *Brassica elongata* subsp. *pinnatifida*, *Euphorbia petrophila*, *Jurinea stoechadifolia*.

In addition, we propose the designation of the validly published *Anthemido troztkianae-Artemision salsoloidis* alliance (Golovanov et al. 2021) as the nomenclature type of the *Anabasietales cretaceae* order (Art. 2b, 8).

Order *Anabasietales cretaceae* Golovanov et al. ex Vasheniak et al. 2024

Lectotypus hoc loco: *Anthemido troztkianae-Artemision salsoloidis* Golovanov et al. 2021.

Diagnostic species: according to Golovanov et al. (2021): *Anabasis cretacea*, *Anthemis troztkiana*, *Artemisia salsoloides*, *Atraphaxis decipiens*, *Crambe aspera*, *Echinops meyeri*, *Jurinea kirghisorum*, *Hedysarum tscherkassovae*, *Lepidium meyeri*, *Limonium cretaceum*, *Linaria cretacea*, *Matthiola fragrans*, *Nanophyton erinaceum*, *Seseli glabratum*, *Zygophyllum pinnatum*.

4.5 Distribution of chalk rocky grasslands within the Eastern European Plain

Chalk rocky grasslands sporadically spread within the steppe zone of the arid climate, on the other hand, occur in the south of the forest-steppe and the north of the semidesert zone and should be considered to be azonal-zonal vegetation (Lavrenko 1961) that differs from plain zonal meso-xerophytic grasslands on deep calcareous soils of the *Festuco-Brometea* and semidesert grasslands of *Artemisieta lerchianae* (Mucina et al. 2016, 2024).

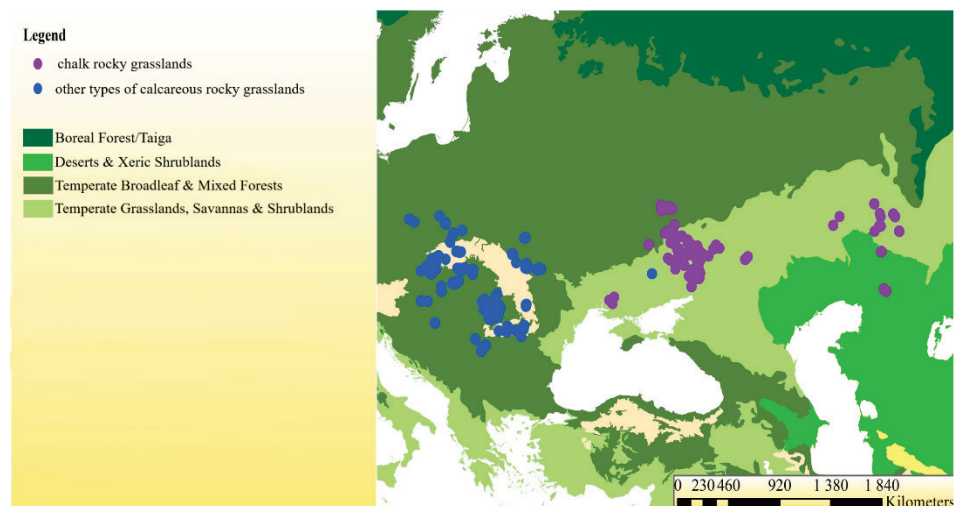


Fig. 9. Biomes and Ecoregions map of the chalk rocky grasslands compared with other types of calcareous rocky grasslands.

Abb. 9. Karte der Biome und Ökoregionen der untersuchten Kalkfelsrasen im Vergleich zu anderen Typen von Kalkfelsrasen.

On the one hand, *Centaureo carbonatae-Koelerion talievii* communities occur in steppe zone, which could be explained by the transitional nature of the alliance, which has a lot of similar features to the *Festucetalia valesiacae* order (*Festuco-Brometea* class) (Roma-shchenko et al. 1996, Poluyanov 2009, Poluyanov and Averinova 2012, Mucina et al. 2016, Didukh et al. 2018). Three plots of *Potentillo arenariae-Linon czernjajevii* Krasova et Smetana 1999, which were initially considered within the *Festucetalia valesiacae* order (Krasova and Smetana 1999), *Cephalario uralensis-Jurineetalia stoechadifolii* order (Vynokurov 2021) and more recently as the *Stipo pulcherrimae-Festucetalia pallentis* order (Mucina et al. 2016, Didukh et al. 2021) and have unclear syntaxonomical affiliation, are floristically very similar to *Centaureo carbonatae-Koelerion talievii* communities. Outliers of chalk rocky grasslands that occur in Right-bank Ukraine (Kherson region), according to the map (Fig. 9), cannot be considered within the *Thymo cretacei-Hyssopetalia cretaceae* order.

On the other hand, *Sileno fruticosae-Nanophytion erinacei* and *Anthemido trozkianae-Artemision salsoloides* communities occur in the arid semidesert zone and are deeply spread within it (Golovanov et al. 2021; Fig. 9). We presume that chalk rocky grasslands could be azonal vegetation, which strongly correlates with the edaphic parameters and is characterised by endemic races or species that are sporadically spread on chalk outcrops within the Eastern

European Plain (Klokov and Dobrochayeva 1974, Tzvelev et al. 1996, Chusova and Didukh 2014). It should be noted that the *Anabasietaia cretaceae* and *Thymo cretacei-Hyssopetalia cretaceae* orders are separated by the Volga Lowland; however, the high terraces of the Don River that occur in the Volga-Don interfluvium, are habitats of *Euphorbia cretophilae-Thymion cretacei* communities (Koroliuk et al. 2021; Fig. 9). Thus, in order to fill the gap between the two orders and find transitional communities within the Volga-Don interfluvium, we aim further to conduct a supraregional analysis of chalk rocky grasslands.

Edaphic and orographic parameters (uplands with chalk outcrops and undeveloped soils on the surface) vary within an arid climate with low precipitation and high evaporation (Didukh 2023). As the continentality indices increase and the indicators of the ombroregime decrease, chalk rocky grasslands change from the transitional *Centaureo carbonatae-Koelerion talievii* alliance to typical *Thymo cretacei-Hyssopetalia cretacei*, *Anabasietaia cretaceae* communities. According to the phytoindication results, continentality and ombroregime correlate with decreased soil humidity, nitrogen content and increased acidity and salt regimes (Fig. 5B). It should be noted that loose and disintegrated substrates of chalk rocky grasslands with a lack of soils differ from the wet, dense substrates of the *Stipo pulcherrimae-Festucetalia pallentis* communities, sub-Mediterranean and supra-oreomediterranean belts of *Drypidetia spinosae*, rocky communities of *Sedo-Scleranthetia* annuals and succulents and sandy grasslands of *Koelerio-Corynephorsetia* (Mucina et al. 2016).

5. Conclusions

We provided a syntaxonomy of chalk rocky grasslands in the Eastern European Plain concluding that all communities belong to the *Thymo cretacei-Hyssopetalia cretacei* and *Anabasietaia cretaceae* orders. They are distinct from other steppe communities and belong to the azonal class *Helianthemo-Thymetia* with a high proportion of chamaephytes. Chalk rocky grasslands have a high presence of stress-tolerant/competitor species (SC) characterised as PSE habitats that occur under extreme conditions. A key aspect that distinguishes *Helianthemo-Thymetia* communities from typical steppe communities is that they form on rocky substrates in the absence of soil, which means that successional processes do not occur here. We consider such communities to be “edaphic-climax”.

The main environmental factors causing the differentiation of the *Helianthemo-Thymetia* communities are the soil reaction, carbonate content, aeration, continentality, cryoregime and light. The *Helianthemo-Thymetia* communities differ from other calcareous rocky grasslands along the moisture, light and nitrogen gradients. The distribution of chalk rocky grasslands is concentrated in the continental arid steppe zone, but they may also be found in the continental arid semidesert and nemoral zone, where climate (temperature, precipitation and continentality) and edaphic conditions (carbonate content, salt regime and soil moisture) vary significantly within three biogeographical zones.

Erweiterte deutsche Zusammenfassung

Einleitung – Kalkfelsrasen, die von bestimmten endemischen Chamaephyten und Hemikryptophyten mit sternförmiger und spinnennetzartiger Behaarung dominiert werden, kommen auf den Kalkfelsen der Flusstäler Osteuropas vor. Sie besiedeln schwach entwickelte Kalkskelettböden (Syrosem, flachgründige Rendzinen) und sind stark vom hohen Karbonatgehalt des Kalkgrundgesteins abhängig. Kalkfelsrasen sind derzeit gefährdet und für den Schutz der Artenvielfalt von großer

Bedeutung. Die Hauptbedrohungen sind Aufforstung, Terrassierung der Hänge und der Abbau von Kreide und Mergel (Kuzemko 2022). Seit der russischen Aggression im Jahr 2014 sind neue Bedrohungen entstanden, die die gefährdeten Kalkfelsenrasen beeinflussen: direktes Verschwinden der Vegetationsdecke aufgrund intensiver militärischer Aktivitäten, aufgegebene landwirtschaftliche Flächen in der Nähe der Hänge von Kalkfelsen und Ausbreitung invasiver Arten. Sie gelten aber gemäß der Berner Konvention als EUNIS-Habitattyp E1.13 (kontinentale trockene, felsige Steppengrasländer und Zwerggestrüpp auf Kalkfelsen) als für den Naturschutz in Europa bedeutsam (Schaminée et al. 2016). Das Hauptziel der vorliegenden Studie war es, die Klassifizierung der Kreidefelsenvegetation in der osteuropäischen Tiefebene anhand eines großen internationalen Datensatzes zu überarbeiten und das Wissen über ihre Syntaxonomie, Ökologie und Verbreitung zu vervollständigen.

Untersuchungsgebiet – Wir haben Grasland auf Kalkfelsen in der Trockenzone der osteuropäischen Tiefebene untersucht. Insbesondere haben wir uns auf zwei unterschiedliche Regionen konzentriert: (1) die Mittellrussische Platte und (2) das Sub-Urale Plateau über einen Klimagradienten hinweg, der die Verteilung und Zusammensetzung der Vegetationstypen innerhalb des Untersuchungsgebiets, in dem Kalkfelsen vorkommen, erheblich beeinflusst. Unser Untersuchungsgebiet umfasst ein breites Klimaspektrum, das von den milden kontinentalen Bedingungen der Ukraine bis zu den rein kontinentalen Bedingungen Kasachstans reicht. Dieser Klimagradient beeinflusst die Verteilung und Zusammensetzung der Vegetationstypen innerhalb des Untersuchungsgebiets erheblich.

Material und Methoden – Um eine Auswahl der Zielpflanzengesellschaften zu erhalten, die der Klasse *Helianthemo-Thymetea* entsprechen, klassifizierten wir den ursprünglichen Datensatz von 3171 Vegetationsaufnahmen mithilfe von Expertensystemen (Willner et al. 2017, Chytrý et al. 2020). Wir verwendeten den modifizierten TWINSpan-Algorithmus (Hill 1979, Roleček et al. 2009): drei Pseudospezies-Schnittwerte – 0 %, 5 % und 25 %, Mindestgruppengröße für die Unterteilung – 10 Aufnahmen, und Whittakers Beta-Koeffizient als Maß für die interne Clusterheterogenität. Die diagnostischen Arten für einzelne Cluster wurden anhand des *phi*-Koeffizienten (Treueschwelle bei *phi* = 0,30) geschätzt, getestet mit dem exakten Test von Fisher ($p < 0,05$) (Chytrý et al. 2002), wobei die Größen aller Gruppen auf gleiche Größe standardisiert wurden (Tichý & Chytrý 2006). Um standörtliche Unterschiede zwischen den Clustern zu untersuchen, verwendeten wir Indikatorwerte vom Ellenberg-Typ und Didukhs Skalen (Didukh 2011, Dengler et al. 2023).

Ergebnisse und Diskussion – Wir haben den Datensatz mit 1643 Vegetationsaufnahmen mit dem modifizierten TWINSpan-Algorithmus klassifiziert. Die TWINSpan-Klassifizierung ergab 13 Cluster. Wir haben 7 Cluster entfernt, die als *Stipo pulcherrimae-Festucetalia pallentis* interpretiert wurden, und uns auf die verbleibenden sechs Cluster als die Verbände *Anabasio cretaceae-Agropyrion desertori*, *Sileno fruticosae-Nanophytion erinacei*, *Anthemido trozkianae-Artemision salsoloides*, *Sileno supinae-Artemision hololeucae*, *Euphorbio cretophilae-Thymion cretacei*, *Centaureo carbonatae-Koelerion talievii* konzentriert. Die Gesellschaften unterscheiden sich deutlich entlang der Gradienten der Klima- und Bodenparameter. Wir haben 7 Cluster zurückgegeben, die als *Stipo pulcherrimae-Festucetalia pallentis* interpretiert wurden und von der Hauptanalyse zum Vergleich von Umweltmerkmalen, Lebensformen und Verteilung der Gesellschaften ausgeschlossen wurden. Gesellschaften der Ordnung *Stipo pulcherrimae-Festucetalia pallentis* weisen einen deutlich höheren Anteil an Hemikryptophyten auf, den höchsten im Fall des Verbandes *Seslerion rigidae*. Im Gegensatz dazu sind in Gesellschaften der Klasse *Helianthemo-Thymetea* Hemikryptophyten viel weniger vertreten, aber der Anteil an Chamaephyten ist wesentlich höher. Wir haben einen aktuellen syntaxonomischen Überblick über die Gesellschaften der Grasländer auf Kalkfelsen in der osteuropäischen Tiefebene gegeben (vgl. Romashchenko et al. 1996, Didukh et al. 2018, Golovanov et al. 2021). Es wurden Übergangsgesellschaften vom *Centaureo carbonatae-Koelerion talievii* beobachtet, die Fragen zu ihrer Klassifizierung aufwerfen. Wir schlagen vor, einige von Didukh (1989), Romashchenko et al. (1996) und Golovanov et al. (2021) ungültig veröffentlichte Syntaxa zu validieren. Die Verbreitung der Kalkfels-Grasländer konzentriert sich auf die kontinentale aride Steppenzone; sie könnten jedoch auch in der kontinentalen ariden Halbwüste und der nemoralen Zone

zu finden sein, wo Klima (Temperatur, Niederschlag und Kontinentalität) und edaphische Bedingungen (Karbonatgehalt, Salzregime und Bodenfeuchtigkeit) innerhalb dreier biogeografischer Zonen erheblich variieren. Wir vermuten, dass es sich bei den Kalkfelsrasen um eine azonale Vegetation handeln könnte, die stark mit den edaphischen Parametern korreliert und durch endemische Rassen oder Arten gekennzeichnet ist, die sporadisch auf Kalkaufschlüssen in der osteuropäischen Tiefebene verbreitet sind (Klokov und Dobrochayeva 1974, Tzvelev et al. 1996, Chusova und Didukh 2014).

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Authors contributions

Y.D. conceived the research project. Y.D. and O.C. provided data on chalk rocky grasslands within the study area. I.V. performed the numerical analyses and wrote the manuscript, supervised by Y.D. I.V. prepared the electronic supplements. O.C. prepared the DCA and box-and-whiskers plots. I.V. and O.C. prepared the figures for publication. All the authors revised the manuscript and agreed on the final version for publication.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. List of aggregate species and definition of their combination.

Anhang E1. Liste der aggregierten Arten und Definition ihrer Kombination.

Supplement E2. Life forms, Grime's strategy for the species list used in the analysis.

Anhang E2. Lebensformen, Grime's Strategie für die Artenliste, die in der Analyse genutzt wurden.

Supplement E3. Algorithm of the Grime's triangle construction.

Anhang E3. Algorithmus zur Konstruktion des Grime-Dreiecks.

Supplement E4. Full synoptic table showing the percentage constancy and fidelity of species of the six clusters.

Anhang E4. Vollständige synoptische Tabelle mit der prozentualen Stetigkeit und Treue der Arten der sechs Cluster.

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Supplement E3. Algorithm of the Grime's triangle construction.

Anhang E3 Algorithmus zur Konstruktion des Grime-Dreiecks.

1. Calculating the indices of CRS using the formulas:

$$Ss=S + (CS/2) + (SR/2) + (CRS/3); Cc=C + (CS/2) + (CR/2) + (CRS/3); Rr=R + (CR/2) + (RS/2) + CRS/3)$$

S is the sum of species with expressed stress-tolerant strategies, C is the sum of species with expressed concurrent strategies, and R is the sum of species with expressed ruderal strategies. The sum values are considered in full.

CS is the sum of simultaneous competitors and stress-tolerant species, CR is the sum of simultaneous competitors and ruderal species, SR is the sum of simultaneous stress-tolerant and ruderal species, and RS is the sum of simultaneous ruderal and stress-tolerant species. The sum values are divided into two.

CRS is the sum of species more or less balanced features of all three strategy types. The sum values are divided into three.

Ss is the sum of all species exhibiting traits of the stress-tolerant strategy, Cc is the sum of all species exhibiting traits of the competitive strategy, and Rr is the sum of all species exhibiting traits of the ruderal strategy.

2. Calculating the ratios between the indicators: Ss: Cc, Rr: Cc, Ss: Rr, proportions of C: S: R = 1.0: X: Y, where X and Y are the proportions of S and R relative to C=1.

3. Displaying the indicators (in percentages) of species ratios on the sides of the Grime triangle, where the vertices correspond to 100%:

- On the C–S side, the point for Cc = $100 \cdot Cc / (Cc + Ss)$, and thus the position for Ss = $100 - Cc$.
- On the C–R side, the position for Rr = $100 \cdot Rr / (Rr + Cc)$, and thus the point for Cc = $100 - Rr$.
- On the S–R side, the position for Ss = $100 \cdot Ss / (Ss + Rr)$, and thus the point for Rr = $100 - Ss$.

The points are plotted on the sides of the triangle and connected. Such a representation becomes an object of further analysis, which we illustrated with specific results.

4. Determining the "centre of mass" of the triangle based on the mean values of the indicators. The "centre" corresponds to point N (x, y), whose coordinates are located at the intersection of its medians. As is known, the point where the medians intersect divides each median in a ratio of 2:1, starting from the vertex. For this, the indicators of the vertices are projected onto the X-axis (coinciding with the lower side of the triangle) and the Y-axis, which are assigned corresponding values. Then, the position of the "centre of mass" is calculated using the formulas:

- $x = (x_1 + x_2 + x_3) / 3$
- $y = (y_1 + y_2 + y_3) / 3$

These points can be constructed graphically. The obtained positions are overlaid onto the Grime triangle, which shows nine fields and a complex transitional zone configuration (CRS). Additionally, fields are highlighted where descriptions cannot fall (horizontal hatching).

